ECOLOGY

Vol. 36 JULY, 1955 No. 3

OBSERVATIONS ON THE ECOLOGY OF A POLYHEDROSIS OF THE GREAT BASIN TENT CATERPILLAR *MALACOSOMA FRAGILIS*

EDWIN C. CLARK

Laboratory of Insect Pathology, Department of Biological Control, College of Agriculture, Berkeley and Albany, California

INTRODUCTION

The termination of large-scale outbreaks of certain lepidopterous and hymenopterous insects by virus diseases is a long-recognized phenomenon (Steinhaus 1949). In the case of the tent caterpillars, *Malacosoma,* one of the first records of the effectiveness of such diseases appears to be that presented by Davis in 1903. Davis, concerned with populations of the eastern tent caterpillar, *Malacosoma americanum* (F.), believed the infectious agent of a widespread epizootic he observed to be a bacterium or a fungus. From his description of the infected insects it is probable that Davis was actually dealing with what we now know to be a polyhedrosis virus (Clark and Thompson 1954). Following the early observations by Davis, several investigators have considered the role of "wilt" or polyhedrosis disease in the natural control of the tent caterpillars (Howard & Fiske 1911: 98; Glaser 1927; Bergold 1951).

The development of the information on the occurrence of polyhedroses in most members of the genus *Malacosoma* has been traced elsewhere (Clark and Thompson 1954); the present paper is concerned with the survival and transmission of the virus causing a polyhedrosis in the Great Basin tent caterpillar, *Malacosoma fragilis* (Stretch). The isolation and identification of this virus was reported by Steinhaus in 1951.

The mechanisms of transmission of viruses afflicting insects are imperfectly known and understood. Bergold (1953) regards this subject as one of the most controversial in the whole field of insect viruses. Of particular interest in this study is the survival and transmission of the virus between generations of insects that are separated by periods during which no susceptible stage of the insect occurs. In the case of *M. fragilis,* as well as other tent caterpillars, this period is relatively prolonged. The adult moths oviposit in August and September and embryonic development is completed in September and October. The first instar larvae overwinter within the egg chorion. Hatching occurs with the flush of new growth on the host plants in May or June. Thus, there is a period of 9 to 10 months during which no stage of the insect capable of ingesting the virus is present.

During an investigation of the possible use of microorganisms in the control of the Great Basin tent caterpillar, an opportunity was afforded to follow the course and effects of a virus epizootic in a population of *M. fragilis* in nature.

HOST INSECT POPULATION

In 1952, when the present study was undertaken, a population of *M. fragilis* had been known in the Shaver Lake-Dinkey Creek area of Fresno County, California, since 1949. In 1950, 1951, and 1952 the insects were distributed over several thousand acres and completely defoliated host plants were found over much of this area. Snowbrush, *Ceanothus cordulatus* Kell., is the principal host of the caterpillar on this site with a gooseberry, *Ribes roezlii* Regal, apparently as acceptable to the ovipositing moths but much less frequent in occurrence.

In early August of 1952, a polyhedrosis epizootic passed through and destroyed a very large proportion of the caterpillar population. The peak of the epizootic appeared to coincide with complete defoliation of the host plants and near-complete development of the larvae. When the area was examined about 3 weeks following the epizootic, many of the dead insects were found still adhering to the shrubs on which they died. Examination of these cadavers by light microscope disclosed heavy concentrations of polyhedral bodies.

That some of the population escaped the disease was indicated by plants on which fully developed tents indicated infestation by the insect but on which few or no dead larvae could be found. In addition, several pupal cases in which the emer-

gence holes appeared normal were collected, as were four 1952 egg masses.

Transmission and Survival, 1952-53

Two possible means of virus transmission and survival between the 1952 and 1953 insect generations were investigated.

Ovarial transmission. On April 23, 1953, three egg masses deposited in the 1952 epizootic area were collected and returned to the laboratory. These egg masses were tied on seedlings of bitterbrush, *Purshia tridentata* D.C., a natural host of *M. fragilis,* and permitted to hatch in the greenhouse. Hatching occurred on April 26 and the larvae were left to develop on the seedlings.

By May 5, nine days following the hatch, about 20 percent of the larvae of one of the egg masses and about 5 percent of the larvae of each of the other two egg masses were dead. These early deaths could not be diagnosed positively as resulting from polyhedrosis infections. Light concentrations of what to all appearances were polyhedral bodies were present, but, because of their small numbers, the identity of these bodies was not certain.

The rate of mortality increased in all the egg masses, but definite diagnoses could not be made until after the eleventh day. From about this time on, heavy concentrations of polyhedral bodies revealed the virus nature of the disease. By May 20, twenty-four days following hatch, all of the larvae of two of the egg masses had died. Fifteen larvae of the third brood were alive and apparently healthy.

Host plant contamination. Examination on April 23, 1953, of *Ceanothus* plants on which caterpillars had died of polyhedrosis in 1952 showed that some of the cadavers were still clinging to the plants. Cadavers were found on or in the old tents and in the forks of twigs and stems. The places where cadavers were most commonly found seemed to be those which would reduce the chance of dislodging of the scales by rain and snow.

Several of the dead cadavers were collected and returned to the laboratory for examination and testing for infectivity. Microscopic examination revealed polyhedral bodies. To test infectivity, the cadavers were macerated in distilled water; blood albumin was added to the resulting suspension; and *Ceanothus* foliage dipped in the suspension was fed, individually, to fifteen *M. fragilis* larvae. All fifteen test larvae died and all deaths could be ascribed to polyhedrosis. Of fifteen control insects, one died of polyhedrosis and two of undetermined cause.

The Epizootic in 1953

Repeated observations were made on the tent caterpillar population on the epizootic area in 1953. The hatch on the site commenced near the end of May. A comparison of the number of tents formed in 1953 with the number present in 1952 indicated that the epizootic of 1952 had reduced the 1953 population to about 10 per cent of the original 1952 population.

An examination on June 15, 1953, showed widespread occurrence of polyhedrosis infections. The insects were in the first, second, and third instars. Inspection of several tents through the area disclosed that roughly one-third of the colonies were completely destroyed by the disease; one-third contained both living larvae and larvae dead of the disease; and about one-third of the colonies were apparently disease-free.

On July 17, counts were made along a ten-foot strip on each side of an abandoned railroad grade traversing the area.[1] Colonies were classified into three categories. Eighty-seven colonies showed no apparent disease; 90 colonies showed at least one dead and at least one living larva; and 96 colonies showed complete polyhedrosis-caused mortality. A study of the apparently disease-free colonies disclosed 18 second-instar, 66 third-instar, and 3 fourth-instar colonies. In comparison with normal development of the Great Basin tent caterpillar in this area, the proportion of fourth-instar insects was very low at the time the count was made. The proportions of second-, third-, and fourth-instar colonies present in mid-July suggests that although some mortality was occurring among the first- and second-instar larvae, the majority of the insects were dying as they passed through the third stage.

Close examination on August 2, revealed no tents which had been developed to the normal size of mature tent caterpillar colonies. No tents that contained living insects were found. Two healthy fifth-instar larvae were found in about an hour of searching. Thus, at the end of the 1953 season the tent caterpillar population had been reduced to negligible proportions; host plants suffered very little defoliation during 1953.

Larva-to-Larva Transmission

A second route of transmission of the virus causing polyhedrosis in *M. fragilis* larvae, transmission between caterpillars of the same generation, was also investigated.

The sites of infection of the polyhedrosis vi-

[1] The writer gratefully acknowledges the assistance of Dr. C. G. Thompson and Mr. J. D. Briggs in the collection of these data.

ruses are known to be blood, hypodermal, fat body, and tracheal-matrix cells. It might therefore be conjectured that the absence of a passageway to the outside of the body of an infected insect would preclude the transmission of the virus to a healthy insect. Once the infected insect dies, however, the disintegration of the body makes the infectious material readily available to other larvae feeding on the host plant.

A field test was carried out in 1953 to determine the possible extent of such transmission during the development of a single generation of the Great Basin tent caterpillar. The test was conducted in the vicinity of Truckee, Nevada County, California, with an *M. fragilis* population infesting bitterbrush. In this test, the foliage near ten colonies of first-; second-; and third-instar larvae was heavily sprayed with a water suspension of polyhedra. Forty-eight hours after this treatment, the tent colonies were removed and each was tied to a host plant on which there was a previously undisturbed colony. The insects that had ingested the virus material were placed sufficiently close to the non-treated colonies to insure intermingling of the two broods.

Within ten days of the original treatment, virus-killed insects were apparent in all the groups. The larvae had become so completely intermingled that, in each of the ten cases, a single tent had been formed and the identification of any larva as to its origin was impossible. It is assumed that this first mortality occurred among the directly treated insects.

As it was desired not to disturb or remove the tents at this time, no counts of living and dead insects were made. Near the end of larval development a comparison of the colonies of insects indirectly exposed to the virus and colonies developing normally showed a marked difference. On the shrubs on which treated larvae were tied only a few, scattered insects were found. Cadavers of virus-killed insects were abundantly evident. On the undisturbed shrubs, the larvae were in the fourth and fifth instars, and, occurring both singly and gregariously, were present in fairly large numbers. At this stage in larval development, the gregarious habit of *M. fragilis* is much weaker than in earlier stages. The scattering of the larger larvae prevented comparative counts of numbers of insects per tent. It was quite clear, however, that in contrast to the undisturbed colonies, the insects which had not been treated directly but which had been exposed to infected larvae had been in large part destroyed.

The detection of slight disease incidence in the control group prompted the examination of several colonies in the immediate area. Of 109 control colonies examined, only eight contained one or more larvae having polyhedrosis symptoms.

Discussion

The observations on the epizootic of polyhedrosis among a population of Great Basin tent caterpillar larvae showed the disease to be capable of sharply reducing the insect population and of near-complete suppression of the succeeding insect generation.

The transmission of viruses causing polyhedroses in insects in some association with the insect egg seems to be generally accepted (Steinhaus 1949; Bergold 1953), although the precise relationship of the virus to the egg (*e.g.*, internal, external, or both) may be in dispute. In the case of the tent caterpillars, Glaser (1927) suggested ovarial transmission of the virus of polyhedrosis of *M. americanum.*

The results of rearing larvae from eggs laid by adults in the epizootic area of this study seem to indicate that overial transmission is an important factor in the epizootiology of polyhedrosis of *M. fragilis.*

Shortly before death from polyhedrosis, larvae of *M. fragilis* hang by the prolegs from the tent, leaves, or twigs on the host plant. About the time of death the body contents are almost entirely liquefied and the integument is extremely fragile. Frequently the weight of the body contents is sufficient to break the integument, thus releasing the highly infectious liquid and permitting it to smear over the site of the insect's death. The cadaver, if undisturbed, may, however, remain intact and be reduced to a mass of spongy or gummy substance which adheres to the site of death. In either case, the liquefied smear or the scale contains infectious virus and this contamination on the plant is a source of infection for healthy larvae feeding on the plant on which other larvae have died.

The collection and demonstrated infectivity of the scales found in 1953 establishes the presence of the virus on the host plant. The virus was not, however, demonstrated on plant material ingested by the insect, a condition necessary for infection. Little information is available on the mechanical spread of insect viruses through the movements of host larvae and associated insects or by other means. Bird (1953) found that the polyhedrosis virus of the European pine sawfly, *Neodiprion sertifer* (Geoffr.) was distributed following its careful application to the trunk of a host tree in a formerly disease-free area. He attributed part of the spread of this disease to such agents as scavenging insects, predaceous and parasitic insects, and birds.

Bird (1954) has also concluded, in contrast to the results of the present study, that little if any of the viruses causing polyhedroses in *N. sertifer* and the European spruce sawfly, *Diprion hercyniae* (Htg.) remains on the host trees through the winter. In view of the differences between the insects which Bird has been studying and *M. fragilis* and in view of differences of the host plants involved, Bird's conclusions are not necessarily contradictory to the present study.

It seems quite likely that if the host plant is contaminated with the highly infectious virus, as was demonstrated in the present study, this contamination may be an important source of infection.

In evaluating the results of the tests on larva-to-larva transmission, it may be noted that three conditions were at a near optimum for the spread of the disease. These three factors were: 1) close intermingling of the infected and non-infected caterpillars; 2) a high ratio of infected to non-infected caterpillars; and 3) infection and death of the directly treated insects early in the larval period. The tests appear to indicate that under these conditions the virus disease may spread rapidly and thoroughly through the caterpillar population on a given plant.

Summary

The tent caterpillars (*Malacosoma* spp.) have been known for some time to be susceptible to polyhedrosis disease. This disease has been observed to be an important factor in terminating widespread outbreaks of the Great Basis tent caterpillar, *Malacosoma fragilis* (Stretch) as well as outbreaks of other members of the genus.

Observations on a polyhedrosis epizootic among tent caterpillars in nature showed the disease to be capable of destroying almost all of the insects present and of preventing the development of a second generation.

Studies on the generation-to-generation transmission of the virus appear to indicate that ovarial transmission plays an important role in carrying the virus through the 9- to 10-month period during which no susceptible stage of the insect is present. Host plant contamination may also be important in this respect. The virus was shown to survive the winter on the host plant and to be a potential source of infection for developing larvae.

Several colonies of young larvae were treated with the virus and then placed on plants on which there were untreated insects. The subsequent death of the insects not treated directly indicated that under the conditions of the test the disease may spread fairly rapidly among the larvae of a single generation.

References

Bergold, G. H. 1951. Notes on polyhedral disease of forest tent caterpillar, *Malacosoma disstria*. Bi-mon. Prog. Rept., Div. Forest Biol., Can. Dept. Agr., **7**(4): 1-2.

———. 1953. Insect viruses. *In* Advances in virus research, pp. 91-139. New York: Academic Press.

Bird, F. T. 1953. The use of a virus disease in the biological control of the European pine sawfly, *Neodiprion sertifer* (Geoffr.). Can. Entomol., **85**: 437-446.

———. 1954. The use of a virus disease in the biological control of the European spruce sawfly, *Diprion hercyniae* (Htg.) Bi-mon. Prog. Rept., Div. Forest Biol., Can. Dept. Agr., **10**(1): 2.

Clark, E. C. and C. G. Thompson. 1954. The possible use of microorganisms in the control of the Great Basin tent caterpillar. J. Econ. Entomol., **47**: 268-272.

Davis, N. F. 1903. The apple tent caterpillar and its life history. Penn. Dept. Agr., Bull. 120.

Glaser, R. W. 1927. Studies on the polyhedral disease of insects due to filterable viruses. Ann. Entomol. Soc. Amer., **20**: 319-342.

Howard, L. O. and W. F. Fiske. 1911. The importation into the United States of the parasites of the gipsy moth and the browntail moth. U.S.D.A. Bur. Entomol., Bull. **91**: 97-102.

Steinhaus, E. A. 1949. Principles of insect pathology. New York: McGraw-Hill, xi + 757 pp.

———. 1951. Report on diagnoses of diseased insects, 1944-1950. Hilgardia, **20**: 629-678.

ANNUAL TRENDS IN COLD HARDINESS OF PONDEROSA PINE AND GRAND FIR

JOHNSON PARKER[1]
Department of Biological Sciences, University of Idaho, Moscow, Idaho

INTRODUCTION

The problem of resistance of conifers to various aspects of low temperature has long been the subject of speculation but not too much research. Some species of conifers, such as grand fir (*Abies grandis* (Dougl.) Lindl.) seem better adapted to high elevations in northern Idaho than species like ponderosa pine (*Pinus ponderosa* Laws). Whether or not winter phases of temperature play a role in this survival is not known. In an attempt to study the low temperature resistance of these two species at various times of the year, the following work was carried out.

METHODS

A cooling apparatus was especially built for this work by the A. B. Hess Co., of Spokane. This consisted of a one gallon capacity circular chamber, eight inches in diameter, surrounded by a one foot thick insulation of rock wool. A hole was provided in one side to permit entry of wires for a thermocouple, and a lid in the top for entry of leaf samples. The lid consisted of an ice-cream well top and this was covered with a two inch thick layer of sponge rubber and another wooden lid. Cooling was accomplished by copper coils wound around the galvanized iron walls of the chamber and connected to a ⅓ h.p. compressor using low-temperature Freon.

Branches of the above-mentioned species were obtained from 50-year old trees near Gnat Creek on the south side of Moscow Mountain at about 2,770 ft. elevation. Only one individual of each species was sampled, successive samples being taken from the same trees. Branches were brought into the laboratory in about a half an hour and leaves placed in test tubes after being cut from branches. Test tubes were then immersed in ethylene glycol contained in a DeWar flask.

The process of slow cooling was as follows. The glycol had been previously cooled to 5°C. and the flask with six test tubes containing the leaves was kept at this temperature for 12 hours. The flask was then placed in the chamber of the low-temperature apparatus and a thermocouple junction placed in one of the test tubes. All test tubes were stoppered with corks and the wires led out to a cold junction and microammeter which had been previously calibrated. In bringing the leaves down to a relatively low temperature, the thermostat was first set for —10° C. in the chamber. After the temperature inside the test tubes had fallen to this point, the thermostat was moved down another 15°C. In this way a cooling rate of about 1°C. per hour was obtained in the test tubes; this rate was used in studies of Siminovitch and Briggs (1953). Although we have recorded 6°F. change per hour in Moscow in sheltered thermographs, it was believed best to use slow cooling in the main studies, since this theoretically reduces the complicating factors which enter during fast cooling.

Although the colder air tended to sediment in the test tubes, leaves extended to the bottom and the effect of the treatment was observed at the lowest point in the tubes. The thermocouple also reached to the bottom of the tubes.

Warming was accomplished as follows. After the temperature in the test tubes within the cooling apparatus had reached a certain point, a pair of test tubes was removed from the DeWar flask in the freezing apparatus and placed in a second DeWar flask containing ethylene glycol which had been previously cooled to approximately the temperature in the first DeWar flask in the apparatus. The second DeWar flask was then stoppered with cotton and allowed to warm up to room temperature by leaving it on the laboratory table. The rate of warming was rather fast at first but on the average gave a rate of warming of about 1.5° C. per hour.

After the leaves reached room temperature, they were allowed to stand in the open for six hours and then tested by the tetrazolium technique previously described (Parker 1951, 1952, 1953). Ordinarily the "killed" leaves turned a yellowish green, resembling "Javel green" in the Ridgway color tables (Ridgway 1912), but these color changes are not very dependable in the case of freezing treatments. Therefore, tests with 2, 3, 5-triphenyltetrazolium chloride were used exclusively as a determination of viability.

Before the present study was undertaken, considerable experimentation was made on the effects of dehydrating these leaves (Parker 1951, 1952) since slow freezing and simple dehydration have

[1] Aided by a research grant from the University of Idaho.

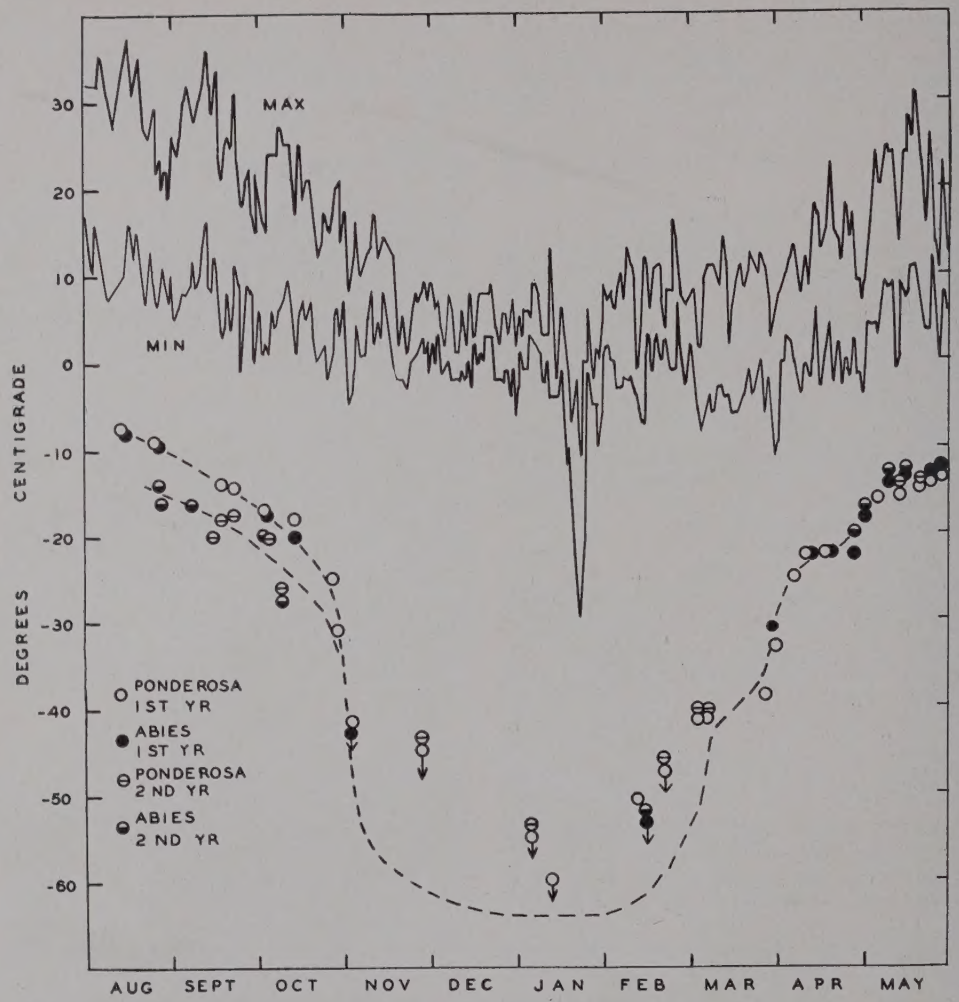


FIG. 1. Maximum and minimum temperatures recorded near the trees sampled are shown above for the year 1953-54. Leaf hardiness (lowest temperature resulting in only slight injury) is shown below. "1st year" refers to leaves that were three months old in August, 1953; "2nd year" to those 15 months old in August, 1953. Arrows on some points indicate that killing was not attained at the temperatures indicated.

certain similarities in their effects (Siminovitch and Briggs 1953). Excised leaves of ponderosa pine left on the laboratory table were found to dehydrate rather slowly but grand fir relatively rapidly. It was therefore considered best to place the leaves in a humid chamber after removal from the freezer before being treated with the tetrazolium chloride. Since excised leaves of these species have been kept in a viable state for as long as three months by keeping them hydrated and weakly illuminated, it was assumed that excision alone was not the cause of viability deterioration with time.

RESULTS

Excised leaves of grand fir and ponderosa pine showed the same general hardiness trends throughout the year. Results are shown in Figure 1. Only in May did grand fir show a somewhat greater sensitivity to cold than the pine. On the other hand, hardiness differences in ages of leaves showed up during the autumn as well as the spring. In the autumn, the current season's leaves ("first year") were more sensitive than the previous season's leaves ("second year"). During the coldest part of the winter, leaves of both species could not be cooled sufficiently to cause them in-

jury by the method described, regardless of age. Only leaves that were held at room temperature for one hour and suddenly plunged into the freezer at —30° C. or were suddenly brought out from —45° C. to room air were damaged in January. During spring, the youngest leaves (now one year old) were more resistant in both species than the previous year's leaves (two year old). By May 31st, new leaves had begun to appear on both species and each of these were resistant to about —10° C. At the same time one year old leaves of pine were resistant to about —14° C. and two year to —12° while grand fir leaves one and two years old were somewhat less resistant (Fig. 1).

One of the most striking things about the data shown in Figure 1 is the sudden increase in hardiness (decrease in minimum killing temperature) for both species in early November. Hardiness also made another rapid change in late winter which may be related to higher maximum temperatures rather than higher minima.

Another thing worth mentioning was the pronounced yellowing of the grand fir leaves during January when they were brought into the laboratory. In all freezing tests, leaves were transferred to the DeWar flasks out-of-doors so that they would not be exposed to the dry, warm room air; but when leaves were brought into the laboratory without protection, and thus suddenly warmed up, they turned a yellowish color in about 12 hours. This was true of all ages of leaves on a single branch. In the field, a similar phenomenon was observed in late January during warm days that followed the cold period shown by the large temperature drop in Figure 1 in January. Yellowing occurred only on the south sides of the grand fir trees. Ponderosa pine showed only slight effects. Only the youngest leaves were affected in contrast to the laboratory results.

Discussion

It would appear from the research described above that minimum temperatures *per se* have little to do with producing a condition of high grand fir abundance and low ponderosa pine abundance at higher elevations in parts of the northern Rocky Mountains. Leaves of both species seemed amply protected against cold during the coldest part of the winter and little or no species difference could be detected. Furthermore, the winter minimum temperature near the top of the Moscow Mountain (5,100 ft.) during the winter of testing (1953-54) was exactly the same as at the location where the trees were sampled (2,770 ft.).

The question then arises as to how great a generalization can be made from the freezing studies described in this paper. In examining the literature one finds few studies made on hardiness of North American conifers. Clements (1938) gave some data for ponderosa pine but this is limited to only a part of the year. A number of papers have appeared on European conifers (Pfeiffer 1933, Cartellieri 1935, Ulmer 1937, Pisek and Schiessl 1946). These studies show certain similarities to our own. For instance, they found a slow late-summer increase in hardiness, a rapid increase in autumn, and then a decrease in hardiness in late winter in spite of continuing low minimum temperatures. However, some of these data are hard to compare to our own since rates of cooling and warming are not always clearly specified. That the rate of temperature change is important was pointed out by Sachs (cited by Sorauer 1934) many years ago and more recently by Pfeiffer (1933) for conifers. The more rapid changes (10° per minute) seem to be more damaging than the slow (1° per hour).

It would be expected, therefore, that sudden changes in temperature might be more damaging to conifers in the field than slow changes, especially when hardiness is not much developed. This is brought out by many publications. Schreiner (1937), for instance, mentioned a drop in temperature of 57°F. in mid-December in northern Idaho, presumably in about six hours, which resulted in near elimination of young ponderosa pine trees of Pacific Coast origin. Rocky Mountain progenies of the same species were practically unaffected. Korstian (1921) described the damage to a number of native and exotic conifers caused by a late spring frost in the central Rockies. Rubner (1921) felt that this occurrence of unseasonal sudden drops in temperature might account for the northward limitation of a number of forest trees in Europe. This is in contrast to the ideas of Shreve (1914) who considered that most vegetation was limited in its northward extent in the northern hemisphere by winter phases of temperature. Münch (cited by Pisek and Schiessl 1946) would seem to agree with Shreve in part, but felt that it was the sudden drops in temperature that caused winter damage to many conifers.

Unfortunately, the effects of winter drying of conifer leaves are often difficult to distinguish from the effects of cold (sudden cold?). Desiccation during the winter would seem to be of great importance if we are to judge by the number of papers discussing it (Munger 1916, Bates 1923, 1924, Iwanoff 1924, Goldsmith and Smith 1924,

Meyer 1928, Schmidt 1936, Clements 1938, Boyce 1938, Curry and Church 1952).

It is therefore apparent that sudden drops in temperature and winter drying are more common causes of damage than the mere occurrence of a particularly low temperature. Sudden rises in temperature are perhaps also not to be ignored. In any case, it would be expected that other factors of the environment, such as total heat sums, precipitation-evaporation ratios, and others might be more controlling in the upper altitudinal limits of ponderosa pine and grand fir in the northern Rocky Mountains than minimum temperatures.

Summary

Leaves of *Pinus ponderosa* Laws. and *Abies grandis* (Dougl.) Lindl. were brought from their natural habitat, cut from the twigs, and cooled and warmed to various temperatures at about 1°C. change in temperature per hour. A specially designed cold chamber was used, having a Freon compressor and copper coils wound around the insulated walls. After cooling and warming the leaves, the tetrazolium chloride test was used to determine viability.

Results showed a slow increase in hardiness in late summer and early autumn, and then a sharp increase in hardiness in early November, coinciding with several nights of temperature near or below freezing. During January, leaves withstood at least −55°C. without damage. Hardiness then showed a general decrease during a warm February but even by late May had not reached the degree of sensitivity of the new needles that appeared at that time.

Differences appeared among different ages in both species, but no appreciable ones between the two species, except possibly in May. In the autumn, the current season's leaves were less resistant than the previous season's leaves (one year older leaves), but in spring the sensitivity of these two sets of leaves was reversed, the one year old leaves being more resistant than the two year old. New leaves in spring were slightly less resistant than older leaves in both species.

References

Bates, C. G. 1923. Physiological requirements of Rocky Mountain trees. Jour. Agr. Res. **24**: 97-164.

———. 1924. Forest types in the central Rocky Mountains as affected by climate and soil. U. S. Dept. Agr. Bull. **1233**.

Boyce, J. S. 1938. Forest pathology. McGraw-Hill Book Co., Inc., N. Y.

Cartellieri, E. 1935. Jahresgang von osmotischem Wert, Transpiration, und Assimilation einiger Ericacean der Alpen Zwergstrauchheide und von *Pinus cembra*. Jahrb. f. wiss. Bot. **82**: 460-506.

Clements, H. F. 1938. Mechanisms of freezing resistance in the needles of *Pinus ponderosa* and *Pseudotsuga mucronata*. State College of Washington Res. Studies **6**: 3-45.

Curry, J. R., and T. W. Church. 1952. Observations on winter drying of conifers in the Adirondacks. Jour. Forestry **50**: 114-116.

Goldsmith, G. W., and J. H. C. Smith. 1926. Some physico-chemical properties of spruce sap and their seasonal and altitudinal variation. Colorado Coll. Pub. Sci. Serv. **13**: 13-71 (Cited by Meyer 1928).

Iwanoff, L. 1924. Über die Transpiration der Holzgewächse im Winter. Ber. der deutsch. bot. Ges. **42**: 44-49, 210-218.

Korstian, C. F. 1921. Effect of a late spring frost upon forest vegetation in the Wasatch Mountains of Utah. Ecology **2**: 47-52.

Mayer, E. 1932. Beiträge zur Kenntnis des winterlichen Wasserhaushalts und der Winterknospen der Bäume. Jenaischen Zeitschrift f. Naturwissenschaft **66**: 535-576.

Meyer, B. S. 1928. Seasonal variation in the physical and chemical properties of the leaves of pitch pine, with special reference to cold resistance. Amer. Jour. Bot. **15**: 449-472.

Munger, T. T. 1916. Parch blight on douglas fir in the Pacific Northwest. Plant World **19**: 46-47.

Parker, J. 1951. Moisture retention in leaves of conifers of the northern Rocky Mountains. Bot. Gaz. **113**: 210-216.

———. 1952. Desiccation in conifer leaves: anatomical changes and determination of the lethal level. Bot. Gaz. **114**: 189-198.

———. 1953. Some applications and limitations of tetrazolium chloride. Science **118**: 77-79.

Pfeiffer, M. 1933. Frostuntersuchungen an Fichtentrieben. Tharandtes forst. Jahrb. **84**: 664-695.

Pisek, A., and R. Schiessl. 1946. Die Temperaturbeeinflussbarkeit der Frosthärte von Nadelhölzern und Zwergsträuchern an der alpinen Baumgrenze. Ber. der Naturw. Med. Vereines in Innsbruck. **47**: 33-52.

Ridgway, R. 1912. Color standards and color nomenclature A. Hoen & Co. Press, Baltimore, Maryland.

Rubner, F. K. 1921. Die Spätfrost und die Verbreitungsgrenzen unserer Waldbäume. Forstwiss. Centralbl. **43**: 41-49, 100-144.

Schmidt, E. 1936. Baumgrenzstudien am Feldberg im Schwarzwald. Tharandter forst. Jahrb. **87**: 1-43.

Schreiner, E. J. 1937. Improvement of forest trees. Yearbook of Agriculture. U. S. Gov't Printing Off., Washington, D. C.

Shreve, F. 1914. The role of winter temperatures in determining the distribution of plants. Amer. Jour. Bot. **1**: 194-202.

Siminovitch, D., and D. R. Briggs. 1953. Studies on the chemistry of the living bark of the black locust in relation to its frost hardiness. III. The validity of plasmolysis and desiccation tests for determining the frost hardiness of bark tissue. Plant Physiol. **28**: 15-34.

Sorauer, P. 1934. Handbuch der Pflanzenkrankheiten. Vol. 1, Teil 1, P. Parey, Berlin.

Ulmer, W. 1937. Über den Jahresgang der Frosthärte einiger immergrüner Arten der alpinen Stufe, sowie der Zirbe und Fichte. Unter Berücksichtigung von osmotischem Wert, Zuckerspiegel, und Wassergehalt. Jahrb. f. wiss. Bot. **84**: 533-592.

A STUDY OF THE OCCURRENCE OF AMPHIBIANS IN RELATION TO A BOG SUCCESSION, ITASCA STATE PARK, MINNESOTA[1]

WILLIAM H. MARSHALL AND MURRAY F. BUELL
Department of Entomology and Economic Zoology, University of Minnesota, St. Paul, Minnesota and Department of Botany, Rutgers University New Brunswick, New Jersey

The occurrence of animals in relation to various stages of plant succession has both fundamental and applied significance. While developing field projects for classwork at the Lake Itasca Forestry and Biological Station in northwestern Minnesota, the authors coordinated portions of the field work by students in a course in animal ecology taught by the senior author and plant ecology taught by the junior author to demonstrate this phase of ecology. The present report summarizes the results of several years of collecting amphibians and sampling plant occurrence in a bog succession that according to Conway (1949) ". . . presents an apparently perfect example of the successional stages of this locality."

The area in which the studies were carried out is located in Bog D as shown by Conway (1949) in her Figure 2. More specifically this area lies in Section 30, T 143 N, R 35 W in Hubbard County, Minnesota.

Field data on amphibians were obtained about mid-August of the years 1949 through 1953 by class members of the animal ecology course. Reconnaissance surveys, as described later, have been made by plant ecology groups at about the same time each year except 1953. Following field work a seminar has been held annually to discuss the current and previous data and their various implications. In 1951, 1952 and 1953 the stomach contents of the frogs collected were examined. Mr. William Tunis, Dr. Herman T. Spieth, and Dr. Alvah O. Peterson identified these materials following preliminary treatment by class members. Detailed results of these and other amphibian food habit studies will be reported elsewhere.

In August, 1953, Mr. A. Grewe and L. D. Frenzel, members of a course in Organisms, Microclimate and Weather under the direction of Dr. Donald B. Lawrence conducted certain studies of the microclimate in the area. The authors appreciate sincerely the opportunity of using these data in the present discussion.

THE VEGETATION

The lake and its associated bog communities, subject of this specific study, lie in a large, continuous but irregular bog complex of small lakes, sedge mat meadows, and bog forests. Conway (1949) published detailed data on one of the sedge mats and its associated forest communities.

Around the bog lake are distinct girdles of vegetation, each successive one taller than the preceding. They can all be seen from the central pond as one looks toward the upland (Fig. 1). First is the sedge mat then come small tamaracks (*Larix laricina*), behind which are large tamaracks and black spruce (*Picea mariana*), then fir (*Abies balsamea*) and black ash (*Fraxinus nigra*), and finally the conifers, mostly red pines (*Pinus resinosa*), of the surrounding upland.

In addition to reconnaissance trips, the structure and composition of the vegetation comprising the successive bog communities have been studied by means of a line transect extending northward from the pond to the upland. Along this line cover in all layers was determined. For the herb and moss layers, cover was determined by estimates, first on the sedge mat and then at every 20-meter point along the line. Shrub and sapling cover was measured by the line intercept method for alternate 10-meter segments of the line. Cover by tree canopy was also measured by the line intercept method but along the entire length of the transect. Although the figures for cover are not included here, the following description is based upon these cover data in addition to the reconnaissance observations of the bog area. Nomenclature is according to *Gray's Manual*, 8th edition (Fernald 1950).

The pond has a very rich growth of aquatics with *Najas flexilis, Potamogeton zosteriformis* and *Lemma trisulca* dominant in August when the bog was studied. Filamentous green algae and plankton forms are abundant.

The sedge mat (definitely floating in August 1952) is particularly unstable at the margin. It is made primarily by *Carex lasiocarpa* var. *americana*. Of the various other species that grow upon it, *Muhlenbergia racemosa* is especially conspicuous throughout and is uniformly distributed, but it is actually low in relative amount. Scattered plants of *Typha latifolia* occur on the mat, in some places forming dense stands, particularly back toward the tamaracks. Widely scattered

[1] Paper No. 3141 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.

FIG. 1. General view of Twin Lakes Bog D. Foreground, sedge mat; beyond the water are shown the sedge mat, tamarack and spruce zones, with pine forest on the upland in the background (From Conway, 1949).

clumps of willows (*Salix* spp.) and bog birch (*Betula pumila* var. *glandulifera*) occur also, especially near the tamarack margin. There is, however, no pronounced shrub-dominated zone at the inner edge of the mat; the tamaracks grow right up to the open sedge mat.

The girdle of young tamaracks immediately around the sedge mat is the wettest, and there the footing is least firm of any part of the bog. The trees shade out *Carex lasiocarpa* and, except for the hummocks at the tree bases, the footing is soft and mucky. Here such plants as *Caltha palustris, Menyanthes trifoliata* and *Smilacina trifolia* are common. Coarse sedges (principally *Carex strictior*) and *Typha latifolia* contribute most to the general aspect of the herb layer but are too sparse to add much firmness to the ground. The scattered shrubs are principally willows and bog birch. The hummocks that have grown up around tree bases are largely composed of Sphagnum. They bear a group of plants most of which are different from the ones that grow in the low area around them. These plants on the hummocks are notably heaths such as *Vaccinium oxycoccus, Pyrola rotundifolia,* and *Ledum groenlandicum.* At the site of the transect the tamarack community is twenty meters wide. Elsewhere, especially between lakes and open mats of the bog complex, it is more extensive.

A community dominated by black spruce with a few, mostly large tamaracks is next behind the girdle of tamaracks. At the location of the transect this is a rather open community with relatively sparse tree cover. There had been a great deal of death and downfall of black spruce. "Witches' brooms" are common and *Arceuthobium pucillum* occurs on a large proportion of the trees. Shrub cover is greater than in the tamaracks as is the variety of shrub species present. In addition to those already mentioned, *Lonicera caerulea* and *Vaccinium pennsylvanicum* contribute appreciable cover. Sphagnum hummocks around tree bases are much larger and many of them have coalesced. Their flora is similar to that of hummocks in the tamarack community. The depressions also have a similar flora, being dominated by sedges (especially *Carex strictior*), grasses (especially *Calamogrostis canadensis*) and *Typha latifolia.* Mosses form an essentially complete ground cover, with species differing on hummocks and in depressions, as Conway (1949) has shown for this same community elsewhere.

The black spruce community is quite extensive in the bog complex as a whole, although at the

site of the transect it is only about 40 meters wide. Where the spruces stand closely, the grasses, coarse sedges and Typha are of little importance or absent. Shrubs are also fewer and the herbs as a whole are sparse, but the moss layer is complete. In other places recently uprooted trees have greatly distributed the surface, creating high root mounds and large pools of water where the trees stood. At such spots release from shading results in rapid growth of shrubs and herbs.

Toward the upland from the black spruce community the vegetation changes. Along the line of the transect balsam fir and black ash become the characteristic trees although with them are black spruces and large tamaracks and also occasional white pine (*Pinus strobus*), paper birch (*Betula papyrifera*) and mountain ash (*Sorbus subvestita*). The tree canopy is more continuous, but at the same time there is a greater development of the shrub layer. Alder (*Alnus rugosa* var. *americana*) and mountain maple (*Acer spicatum*) are the species that contribute principal cover in the shrub layer. The shade is greater than in the other communities and the herb layer is rich in species, some of which are common in upland spruce-fir forests. No one species is dominant but several contribute more or less equally to the cover. The ground is much firmer and drier. Fallen trees and rotting logs are common. The moss layer is less continuous and species of Sphagnum contribute much less. The hummocks are often litter-covered.

Although this represents the typical community at the end of transects farthest from the bog lake, the pattern along the bog margin varies. Locally alder-mountain maple shrub thickets may predominate. In many places, however, there is a marginal bog forest of black ash, especially pronounced in shallow embayments.

These several vegetation types represent fairly pronounced environmental conditions. Not only are there the obvious differences, such as increasing shade at the ground level from the mat to the marginal bog forest, but other studies suggest less obvious differences within and between the communities. There can be little doubt that the bog level fluctuates annually, as it does at Cedar Creek Bog (Buell and Buell 1941). If so, the sedge mat rises readily as the pond level rises in the spring, but the tamaracks are for a while flooded. Also, the depressions between the hummocks of Sphagnum back across the bog are water-filled in the spring. Furthermore, within the communities the ground conditions show wide differences, the depressions having a high pH and the hummocks being characteristically very acid (Conway 1949).

Occurrence of Amphibians

As might be expected, a considerable variety of amphibians was found in this area. During the four years, seven species were collected as follows: leopard frog (*Rana pipiens*), wood frog (*R. sylvatica*), mink frog (*R. septentrionalis*), spring peeper (*Hyla crucifer*), tree frog (*H. versicolor*), swamp tree frog (*Pseudacris nigrita*) and the American toad (*Bufo americanus*). The names used follow those of Breckenridge (1938).

Approximately the same areas were chosen for collecting each year in the center of the broadest bands of plant zonation available. Class members lined up abreast about two feet apart and slowly advanced, catching frogs as they were flushed. As individual frogs were caught, they were placed in containers that were labeled as to location for return to the laboratory. One or two class members acted as tally clerks to record the animals that eluded capture, keep time on each sweep, and determine the acreage covered. Logs or brush piles were not torn up or moved during the chase. The area covered in each zone was usually 20 to 30 feet wide by 100 to 150 feet long and the time spent in each was kept more or less constant at 10 to 15 minutes per area. Collecting was done in the mornings between 9:00 and 11:30 a.m. Following return to the laboratory, all animals caught were carefully examined, measured as to body length, sexed internally, and the stomach contents emptied into watch glasses for examination. The zones of vegetation as described earlier were recorded as: sedge mat, tamarack, spruce, and fir-ash.

During the five collecting sessions, a grand total of 874 frogs was recorded (Fig. 2). Seventeen were not identified; 533 eluded capture but were positively identified; and 324 were caught and returned to the laboratory.

The majority (498) of those which were identified without capture were leopard and wood frogs. These two frogs differed considerably in size (the former always being over 40 mm. and the latter mostly less than 30 mm. in length) and commonly occurred together only in the tamarack zone. The activities of these frogs in escaping were distinct and quite different from those of the other species listed. Each year the class members had handled three to five hundred wood frogs in previous weeks and were thoroughly conversant with the field aspects of this animal. Therefore, it is felt that the identification of escaped frogs can be relied upon.

Examination of Figure 2 indicates certain relationships between the occurrence of frogs and the plant zones. It can be stated that these variations

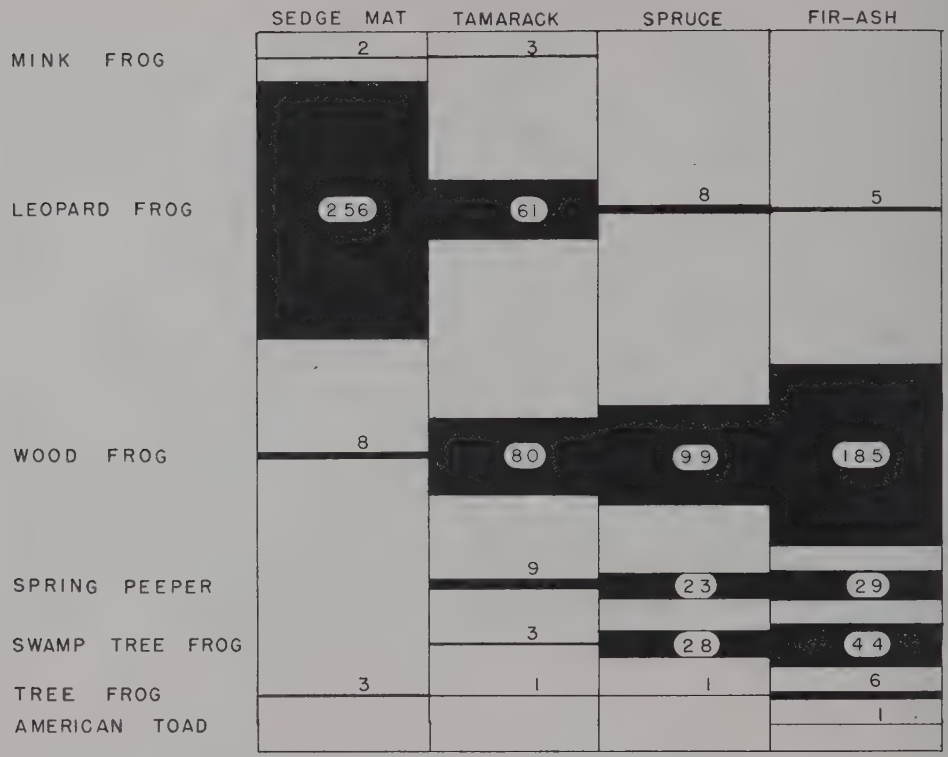


FIG. 2. The occurrence of amphibians in the four vegetation zones of Twin Lakes Bog D for the years 1949 through 1953.

in occurrence were relatively constant from year to year.

The mink frog was observed in the open water areas of the central pond but accurate records were not obtained as the margin of the sedge mat was difficult to approach. The five individuals recorded in the drives were in the wettest of the zones.

The leopard frog was found most frequently in the sedge mat and somewhat less commonly in the very wet tamarack zone. Its occurrence in the other two zones was probably accidental.

The wood frog occurrence varied in the opposite fashion from that of the leopard frog. Its presence in the sedge mat was probably accidental with numbers increasing sharply in the tamarack and spruce zones and then almost doubling in the fir-ash.

The spring peeper was found in the tamarack, spruce, and fir-ash zones with numbers in the first zone much less than in the latter zones.

The swamp tree frog was found primarily in the two zones farthest from the central pond.

In direct opposition to the distribution of the mink frog, the only toad collected was found in the fir-ash.

The tree frog was found very sparingly in each of the zones. All specimens were small bright green animals of the year. Probably collecting methods for this frog, which is both arboreal and a past master at concealment, were entirely inadequate.

It should be stated here that areas on the adjacent dry upland slopes supporting chiefly red pine were searched several times in the earlier years and only a very few wood frogs seen.

Since the bog area is undoubtedly undergoing changes with the years, the data on occurrence of amphibians in the plant zones by each year were examined in detail. The only consistent and differential change noted was the reduction in numbers of wood frogs observed in the sedge mat and tamarack zones. Other data indicated either a consistency in numbers where a significant volume of data was concerned, or an inconsistency

where chance occurrence was found as indicated by only a few individuals in different years.

Amphibian Food Habits

The possibility that differences in food preferences coupled with the distribution of foods by vegetative zones might account for the amphibian distribution was partially investigated by examining the stomachs of 273 frogs. A total of 67 different identifiable items was recorded in the 261 stomachs containing food. Gastropods were determined to genus, insects to order or family, and arachnids to order. Table I summarizes the data by presenting the number of stomachs of the four common frogs in which the three most abundant foods for each species in each vegetation zone were found.

Table I. *Number of stomachs containing the three most abundant food items in each vegetation zone for the years, 1951, 1952, 1953*

	Leopard frog	Wood frog	Swamp-tree frog	Spring peeper
Sedge Mat	(32)*	(1)	(0)	(0)
	Formicidae 12	Formicidae 1		
	Araneida 11	Carabidae 1		
	Ichneumonidae 9	Cicadellidae 1		
Tamarack	(22)	(29)	(2)	(3)
	Formicidae 5	Formicidae 12	Formicidae 2	Aphidae 2
	Araneida 5	Carabidae 9	Diptera 2	Culicidae 2
	Ichneumonidae 3	Ichneumonidae 5	Arachnida 1	
Spruce	(2)	(37)	(16)	(12)
	Formicidae 1	Formicidae 18	Formicidae 8	Lepidoptera 6
	Acarina 1	Zonitoides 10	Diptera 4	
	Zonitoides 1	Coleoptera 7	Araneida 3	Araneida 4
	Silphidae 1			Aphidae 3
Fir-Ash	(1)	(51)	(21)	(20)
	Diptera 2	Formicidae 15	Formicidae 7	Tipulidae 5
	Araneida 1	Araneida 10	Cicadellidae 4	Mycetophilidae 3
		Carabidae 6	Lepidoptera larvae 6	Araneida 3
	Zonitoides 1	Tipulidae 6		
Total Number Stomachs	57	118	39	35

*Figures in parentheses show number of stomachs containing food items.

Examination of this table indicates that the foods most commonly taken by the leopard frog, wood frog, and swamp tree frog were very similar in all four zones. The spring peeper on the other hand exhibited different food preferences than the other three amphibians. Unfortunately, the availability of these and possibly other foods could not be determined.

Amphibian Populations

The possibility of general population differences in each zone arises. The data on the time spent and the area covered in each plot in the years 1950 through 1953 were applied to the total number of frogs identified and/or captured each year by vegetation zone so as to give a figure on the number of frogs per man hour and per acre. Population estimates varied from approximately 5 to 90 animals seen per man hour (Table II). No particular claim can be made for their accuracy. However, except for the year 1950, in all four zones the numbers of frogs seen per man hour were roughly of the same order. In 1950, the ash-fir and sedge mat communities showed high concentrations of frogs in contrast to the tamarack and spruce samples.

Table II. *Frogs seen per man hour for each vegetation zone by years*

	1950	1951	1952	1953
Sedge mat...	92.2	8.4	32.2	13.0
Tamarack...	31.5	8.6	13.8	4.8
Spruce.....	31.2	19.5	29.5	12.0
Ash-Fir.....	77.5	15.7	26.0	11.5
Average.....	58.3	10.5	25.4	10.3

Since these data represent largely leopard and wood frog numbers, a further analysis of these two species was made by year and vegetation zone. The average body length of the leopard and wood frogs caught was compared to the number caught per man hour. In every case but two (of eighteen series of data) either a high number of frogs taken per man hour occurred when the size of the frogs indicated that chiefly frogs metamorphosed in the same year were being handled; or a low rate of catching occurred when the size of the frogs indicated one or two-year old individuals were taken. This is interpreted as showing that the success of reproduction (in this case after metamorphosis) determined the population level each year.

The Microclimate

Studies made by Grewe and Frenzel indicate a few of the differences in the physical factors of the vegetation zones. Stations were set up in the sedge mat, tamarack, and fir-ash zones and visited daily at seven a.m. and six p.m. for the period July 30 to August 5, 1953. Records taken were daily atmospheric temperature extremes at ground level, substratum temperature 6-10 cm. below the surface, light intensity above the ground level, wind velocity, daily evaporation rates, and vapor pressure deficit. During the week, clear and rainy days occurred in nearly equal duration. The quantitative results of some of these preliminary investigations are summarized in Table III, and are suggestive of the summer-time conditions in these habitats. It is realized that other factors are also acting in an unknown fashion.

TABLE II. *Data on microclimate at three stations in the bog (July 30-August 5, 1953)*

	Mean Seven-Day Temperatures				Vapor Pressure
	Air		Substratum		
	Max.	Min.	p.m.	a.m.	Deficit 6 p.m. Aug. 1, 1953
Sedge	83	54	73.8	70.2	9.5
Tamarack	76	58	63.6	61.8	7.8
Fir-Ash	72	58	63.0	61.1	4.7

Examination of these data shows certain sharp differences between the sedge mat and the other two stations. For the period studied both the maximum air temperature and the substratum temperatures are considerably higher in the sedge mat. However, the minimum air temperature is slightly lower. The daily range of temperature was consistently higher at the sedge mat than in the tamarack and fir-ash stations. The vapor pressure deficit for the daylight hours of August 1 shows a nearly similar difference between each station, with the sedge mat having the greatest deficit.

The information on other weather elements is more difficult to summarize. The sedge mat received far more incident light than did the forest floor in the other two stations. All recorded wind velocities were very low but most often the highest velocities were measured on the sedge mat. On clear days the day-time rate of water loss from black- and white-bulb atmometers was highest at the sedge mat.

Presuming that the data available are indicative of general summer conditions, then the maxima and range of temperature, vapor pressure deficit, light, wind velocity and rate of water loss are greater in the sedge mat than in the other two zones. In the case of the substratum the temperature is considerably higher in this zone than in the other two.

DISCUSSION

It must be pointed out that in Minnesota, collecting during August does not involve breeding frogs. From other local studies on the wood frog and general knowledge of the leopard frog it is thought that most of these animals had metamorphosed at least three to five weeks previously and had been moving about in suitable habitats more or less erratically since that time. However, undoubtedly the central pond of the bog is the major breeding site for the leopard frog, and a small pond created by an old woods road fill near the fir-ash plot serves a similar function for the wood frog. These two sites are adjacent to the vegetation zone in which most individuals of these species were found. It is thought that nearly all, if not all, the swamp tree-frogs and spring peepers were adult animals. Although the proximity to breeding sites is a possible complicating aspect (particularly in 1950), it is thought that the occurrence represented the preference of the adult form of these species for the specific vegetation zones during the non-breeding period.

It seems evident from the similarities in stomach contents that food preferences did not play a part in determining the difference in occurrence between the leopard frog and the wood or swamp tree frogs. Food preference may have been important in the case of the spring peeper, as the groups of insects represented were different than for the other three species.

Although other unmeasured physical or biotic factors may play important roles, the microclimate data could well account for the differences between the leopard frog and the other species. In discussing factors limiting geographic distribution in frogs, Moore (1949) states "there is a general feeling that the most important factors are temperature and moisture." The available data on these two factors in the Twin Lakes bog may profitably be examined and compared with the information on the occurrence of the leopard and wood frogs. It is necessary in this case to think not only of actual temperatures but also of the range of temperature. A further consideration is the probable adaptability of the animals themselves.

The sedge mat (with its higher substratum temperatures) may have been preferable to the leopard frog which is more southerly in distribution than the wood frog. Here, also, is the zone with the widest range of atmospheric temperatures. The leopard frog, as Stebbins (1951) suggests, is a "highly adaptable species" and possibly withstands such variations more easily than the wood frog—particularly when the change is one towards higher maxima rather than lower minima. This daily temperature variation may have inhibited the wood frog from remaining on the sedge mat.

Atmospheric moisture conditions were apparently drier in the sedge mat. When one considers the westward range of the leopard frog across the drier prairies which do not support the wood frog, this difference also may explain the occurrence of these two species.

The occurrence of the two other amphibians (swamp tree frog and spring peeper) would seem to coincide with both the atmospheric tempera-

ture gradient and the increasing amounts of moisture available in the air.

Another plausible explanation may be in the "life form" preferences of the species. The leopard frog, known also as the grass frog, was found in the zones where grass-like plants dominated the ground cover. At the other extreme the swamp tree frog and spring peeper, both members of the tree frog group and good climbers, were found where a low growing herbaceous and shrubby layer of plants occurred. The wood frog, an animal of the bog forests in this area, was most abundant where a large variety of fallen logs and brush piles occurred.

Possibly the most important facet of the "life form" in this case is escape cover. The leopard frog was found chiefly where there was nearby open water or numerous pools to hide in. In fact, on the sedge mat most of the frogs escaped by making a bee line for the open pond in spite of efforts to intercept them. The wood frog more commonly jumps to holes under hummocks, logs and brush piles for escape cover. The other two frogs appear to depend more completely on protective coloration to conceal them in herbs and shrubs rather than on active escape.

In the authors' opinion, these factors of the character of the ground vegetation and escape cover which, of course, themselves are a reflection of the microclimatic conditions, may well have a considerable influence on the occurrence of these animals in the different communities of this bog succession.

Summary

1. Through the coordination of field work by classes in animal and plant ecology, data on the occurrence of plant and amphibian species in a typical northern Minnesota bog succession were obtained during August of each summer from 1949 through 1953.

2. The various bog communities in the Twin Lakes bog of Itasca State Park are described as girdles of vegetation with sedge mat, tamarack, black spruce, and finally, fir and black ash in successive bands from the central open water area to the adjacent dry upland. Trees, shrubs, herbs, and mosses are listed for each zone based on data from frequent reconnaissance trips and a transect run through the narrowest portion of the bog each year.

3. The occurrence of 874 amphibians, representing seven species, is recorded in relation to the four bog communities.

4. The most abundant foods found in the stomachs of 261 amphibians are reported by amphibian species and plant zones. These data show similarities for the leopard frog, wood frog and swamp-tree frog, but differences for the spring peeper.

5. Population estimates based on frogs caught per man-hour indicate that success of reproduction determined the population level in all zones each year.

6. Certain microclimatic data showed sharp differences between the sedge mat and the tamarack and fir-ash zones. The former had higher maximum air and substratum temperatures but lower minimum air temperatures. The daytime vapor pressure deficit, incident light, wind velocities, and rate of water loss were highest on the sedge mat.

7. It is thought that the data reported on frog distribution in the bog indicate in part the effects of microclimatic influences on the frogs; in part the influences of cover and life forms of vegetation; and in part the relative abundance of escape facilities for non-breeding frogs.

References

Breckenridge, W. J. 1938. Reptiles and amphibians of Minnesota. Minneapolis: University of Minnesota Press, 202 pp.

Buell, M. F. and H. F. Buell. 1941. Surface level fluctuations in Cedar Creek bog, Minnesota. Ecology, **22**: 317-321.

Conway, V. M. 1949. The bogs of central Minnesota. Ecol. Monogr., **19**: 173-206.

Fernald, M. L. 1950. Gray's manual of botany, 8th edition. American Book Co., 1632 pp.

Moore, J. A. 1949. Patterns of evolution in the genus *Rana*. *In* G. L. Jepson *et al.*: Genetics, Paleontology, and Evolution, Princeton Univ. Press, pp. 315-338.

Stebbins, R. C. 1951. Amphibians of western North America. Berkeley: Univ. of California Press, 539 pp.

THE CLIMATES OF SOUTH BASS ISLAND, WESTERN LAKE ERIE

James L. Verber
Ohio Department of Natural Resources, Division of Shore Erosion, Sandusky, Ohio

Lake Erie has a pronounced effect upon the climate of the islands in the lake and the adjacent mainland as shown by a study of the climate of South Bass Island. Lake Erie is the shallowest of all the Great Lakes, the average depth being 60.7 feet. South Bass Island is situated in the western basin of the lake which has the least depth and is the warmest part of the lake in summer (Millar 1952).

The islands, when compared to nearby mainland stations, show variations in temperature, precipitation, frost-free periods and the amount of solar radiation received. South Bass, more popularly known as Put-in-Bay, has one of the longest records among weather stations in the Great Lakes region.

Leighly (1941) discussed the influences of the Great Lakes on the temperature of the Great Lakes Drainage Basin, but did not show such detailed changes as those that occur within 50 miles of the lake. Leighly states that the effect of Lake Erie on the temperature is slight, producing only a small but noticeable change on the adjacent land. However, a short distance from the lake the effects are almost negligible.

Lake Erie and the other Great Lakes have a climatic variation which is unlike the land regions around them. The annual mean temperature range is greater, the daily range between the maximum and minimum temperatures is smaller, the precipitation less, wind velocities are greater, and the frost-free seasons are longer. Freeman (1926) and Horton and Grunsky (1927) both discussed the variations of the climate of the Great Lakes as compared to the adjacent mainland. These variations are directly related to high specific heat of the water. The climate around the lakes affects the type of land use and the flora of the nearby regions.

Core (1948) states that the islands have plant associations quite different from the adjacent mainland. South Bass Island has a predominant hackberry-blue ash association, two species of trees which are extremely drought-hardy and thrive on thin limestone soils.

Put-in-Bay has had a "co-operative" status with the U. S. Weather Bureau since May, 1916. Several instruments have been added or changed since that time and the records are fairly complete to date. From June, 1944, to August, 1948, thirty-seven temperature stations were maintained at various times on South Bass Island and a study of the thermal microclimates was made. This program was under the direction of Dr. T. H. Langlois. The following pieces of equipment, which are checked periodically by the U. S. Weather Bureau, are maintained and operated at the F. T. Stone Institute of Hydrobiology, Put-in-Bay, Ohio: maximum-minimum thermometers, automatic recording rain gage, recording anemometer, solar radiation recorder, and automatic recording barometer.

The data gathered by some of these instruments are routinely submitted to the U. S. Weather Bureau; they are used here to show the macroclimatic differences between Put-in-Bay and nearby mainland stations, and to demonstrate some of the patterns of microclimates on South Bass Island. All temperatures reported are in degrees Fahrenheit.

I wish to thank Dr. T. H. Langlois and Dr. J. Verduin of the F. T. Stone Institute of Hydrobiology and Dr. Guy Harold Smith, Dept. of Geography, The Ohio State University, for their aid in the preparation of this paper.

The Macroclimate

The macroclimate study is principally used to show the difference in the climate of the island as compared to mainland stations and to point out some of the factors which cause the difference. Put-in-Bay (Figure 1) is approximately 3.5 miles long, trending in a northeast-southwest direction. The widest part of the island is about 1.5 miles. The topography of the island (Fig. 4) is gently rolling. East Point and the central part of the main island are relatively flat compared to the extreme southwest portions.

Productivity

Core (1948) used the following tentative classification for the plant communities. The oak-maple-basswood association, hackberry-blue ash association, abandoned fields, cliffs and rocky shores, and gravel beaches. This does not include the aquatic vegetation.

Core states that the original heavy forest growth is definitely related to the soil types of the island. In the regions of Catawba and Toledo soils, an oak-maple-basswood association (*Quercus alba* L. —*Acer saccharum* Marsh.—*Tilia americana* L.) was prevalent, occupying the more humid sec-

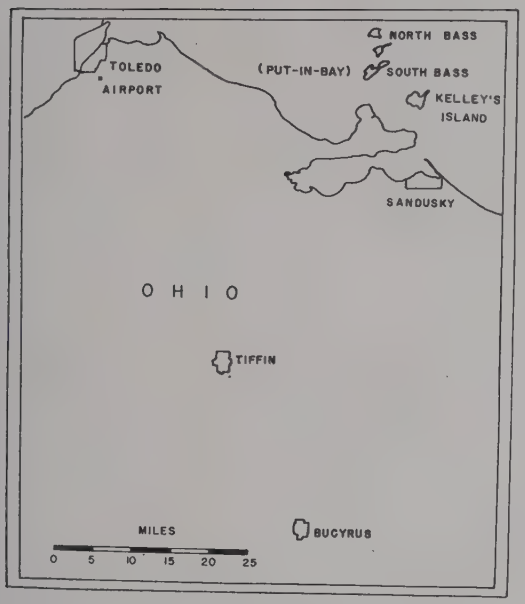


FIG. 1. Location of South Bass Island in relation to the adjacent Ohio mainland.

tions of the island. On the relatively immature Randolph soils and the drier sections of the island there is a hackberry-blue ash association, (*Celtis occidentalis* L.—*Fraxinus quadrangulata* Michx.) The latter is much more prevalent and occupies almost ⅖ of the main island. Core states that there is a "remarkable abundance of hackberry" with almost no other trees existing. Formerly, red cedar (*Juniperus virginiana* L.) was one of the most abundant species of trees on the island, but much of it has now been lumbered. This species does very well on the thin limestone soils on the island. The main plant association, the hackberry-blue ash, and the red cedar, are attributed mainly to the thin soils of the island. The U. S. Department of Agriculture, Yearbook of Agriculture (1949) states that these particular species of trees are extremely drought-hardy. It may be that in addition to the thin soils, the small amount of rainfall during the summer months and high wind velocities are just as important in maintaining this type of plant association, whereas with an abundance of precipitation another type of association might occur.

The principal land-use on South Bass Island is viniculture, with over 270 acres in vineyards. Economic reasons favor the conversion of grapes into wine. The long growing season and high solar radiation in summer produce a grape with a high sugar content. The Catawba grape, used extensively on the island, is a long-maturing, very sweet grape, producing an excellent white wine.

Moseley (1899) found that several plant species in the Sandusky Bay region and the island do not occur in the north-central and central parts of Ohio, but are in the southern part of the state. He stated that the protection against frost tapers off sharply as one leaves the region near the lake and thus certain species cannot survive.

Temperature

The mean annual temperature of Put-in-Bay on South Bass Island, is 50.6°. The most noticeable characteristics of the temperatures are: the high mean midsummer temperature, 74.8°, and the low mean winter temperatures 26.8°, and small monthly range betwene the maximum and minimum temperatures, 13.7° range at Put-in-Bay compared to 21.5° at Bucyrus.

The mean July temperature is 74.8°. Table I, shows the mean monthly range between the maximum and minimum temperatures. Within 50 miles of the lake, at Bucyrus, Ohio (Fig. 1) the temperature range is greater by 7.8°. The daily fluctuations in temperature at Put-in-Bay are not so large as at mainland stations. The data in the first column represent the average for an entire year.

TABLE I. *Climatic variations within 50 miles of Lake Erie**

Station	1950 Aver. mo. range max.-min. temp. (°F)	Temp. (°F) Jan. aver.	Temp. (°F) July aver.	Distance from L. Erie (miles)	Mean precip. (inches)	Frost free season (days)
Put-in-Bay	13.7	26.8	74.8	0	28.99	205
Sandusky	15.9	27.0	74.0	1	32.05	194
Toledo	18.8	26.9	74.0	15	32.11	185
Tiffin	19.5	27.9	73.8	30	36.99	162
Bucyrus	21.5	27.7	73.6	50	38.39	154

*SOURCES: U. S. Dept. of Agric. (1941), U. S. Weather Bureau (1950).

Columns 2 and 3 of Table I, January and July respectively, show that the differences between the mean temperature of the coldest month and the warmest month is the greatest at Put-in-Bay of any of the five stations. In many cases, the frozen lake surface accounts for the colder winters. The greater solar radiation at Put-in-Bay than other stations at the same latitude in summer probably accounts for the higher mean temperatures in July. The hottest days of the month show higher temperatures on mainland stations than at Put-in-Bay, as is implied in the data of column 1.

The great thermal stability of the water acts as a damper against sudden heating or cooling. The temperature during the summer has reached the 100° mark in 6 out of 38 years with a record high of 104° (June, 1934; July, 1936). During

the winter the temperature has dropped below 0° in 15 out of 38 years.

The lowest minimum temperatures of —19° and —15° have both been recorded in February. An ice cover, usually formed in January and lasting through February, around the island region may act as an insulator between the warm water and the cold air. This produces enough of a thermal change to make February colder than January. The ice cover makes it possible for greater cooling of the air mass over the lake to occur at night than could possibly happen when the lake was free of ice. During the past six winters (1947 to 1953) the lake was frozen during January and February three times. The mean temperature during the open periods for the two months was 32.8° whereas during the ice covered period it was 27.8°. It is exceptional that the lake is free from ice during these two months.

During the transition months of spring and fall, April to June, and October to December respectively, great thermal changes occur which are characteristic of microthermal climates. In spring, the island temperatures are 2 to 3° lower than Toledo whereas in the fall they are 2 to 3° higher. The island stations usually show a higher monthly mean temperature than Toledo. The data for Put-in-Bay show that the greatest changes occur during April and May when the mean temperature increases 12° and during October and November when there is a decrease of 13.1°. The annual range of temperature for the islands, excepting Kelley's Island, is greater than at the Toledo station. This is chiefly due to the higher summer temperatures.

Precipitation

One of the seeming anomalies of the climate is the decrease of precipitation as one approaches the lake. Table II shows the variation in precipitation for the islands and four mainland stations (see Fig. 1), with a progressive decrease from Bucyrus to South Bass. Alexander (1924) shows that North Bass Island, for the years recorded, has a smaller annual amount of precipitation, 26.70", than South Bass Island. The decrease occurs during the same seasons as that of Put-in-Bay, in the midsummer and midwinter. Horton and Grunsky (1927) noted that rainfall on the islands was less than shore stations in summer and winter. They also noted that islands which had a relief (such as some in Lake Superior) also had an increased precipitation. The monthly distribution of precipitation shows two periods of decrease, one in midwinter, during the season of snowfall and the other is in summer, during the period of convectional thunderstorms.

Cyclonic storms of frontal origin, which cover large areas and bring general precipitation in spring and fall do not result in a marked decrease in the amount of rainfall at Put-in-Bay as compared to mainland stations. Thunderstorms, however, show a tendency not to produce precipitation while over the lake, or they frequently seem to be deflected around the lake.

The following explanations have been offered to account for the decrease in precipitation. Day (1926) suggested that the lower rainfall may be due to higher wind velocities over the rain gauges. This is certainly possible in the winter season on the island. Horton and Grunsky (1927) referring to Dines say:

> "The moisture-bearing air layers causing rain by their ascent are increased in thickness in direct proportion as their velocity is decreased as they blow on the shore from the water surface. The center of gravity of the moisture-laden air is thus raised. The effect is the same as that of an upward deflection of the air current, which is the most common cause of rain. Conversely, if a moist air layer flows from a rough on to a smoother surface, with resulting increase in velocity, its depth or thickness is decreased and the effect is the same as in the case of descending air current."

Trewartha (1943) states that there is a great inequality of heat absorption and radiation between the land and water surfaces. Because such

TABLE II. *Average monthly precipitation at Put-in-Bay and surrounding area**

Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
North Bass	1.87	1.29	2.22	2.56	2.44	2.71	2.47	2.24	2.79	2.05	2.09	1.97	26.70
Put-in-Bay	1.96	1.51	2.37	3.00	3.05	3.00	2.44	2.78	2.71	2.20	1.99	1.98	28.99
Kelley's Island	1.82	1.74	2.62	2.80	3.20	3.45	3.33	2.47	3.24	2.28	2.59	2.20	31.74
Sandusky	2.45	1.81	2.80	2.73	2.93	3.42	3.32	3.05	3.08	2.37	1.95	2.13	32.05
Toledo	2.39	1.89	2.86	3.04	3.11	3.30	2.82	2.98	3.08	2.32	2.02	2.39	32.11
Tiffin	3.00	2.25	3.44	3.35	3.62	3.69	3.74	2.99	3.30	2.70	2.30	2.61	36.99
Bucyrus	3.16	2.26	3.36	3.28	3.59	4.04	4.12	3.16	3.29	2.94	2.55	2.64	38.39

*SOURCES: Alexander (1924), U. S. Dept. of Agric. (1941).

a great inequality exists, a zone of turbulence is created at the water-land boundary. The zone of turbulence operates in two ways, by deflection and elevation. A thunderstorm approaching the lake may be deflected so that it moves around the edge of the lake. This so-called diversion may be deflection produced by the zone of turbulence. Supporting the concept of deflection is the high rate of solar radiation over the lake in summer (Fig. 2) which suggests a conspicuous absence of clouds.

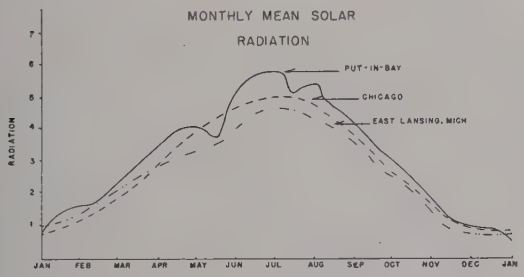


FIG. 2. Monthly mean solar radiation for Put-in-Bay and other stations at the same latitude.

On the other hand, because of the lower temperatures over the lake as compared to the land during the day, thunderstorms cannot maintain their energy over the lake. Thus, it is possible that a very stable air mass is associated with the lake. High daily temperatures are not produced over the lake as the lake absorbs and releases heat very slowly. Horton and Grunsky quote a letter from Dr. C. F. Brooks:

> "In the case of a summer thunderstorm rain, dwindling as the storms approach the shores on the west sides of the lakes, the rainfall over the lakes can probably be estimated by continuing the decrease out on the lakes."

This is clearly shown in the figures of Kelley's Island, Put-in-Bay and North Bass Island. These three islands are progressively farther from the mainland, Kelley's Island having 31.74", Put-in-Bay 28.99", and North Bass with 26.70" of average annual precipitation.

Supporting the theory of stability over the lake in the daytime is the work of Humphreys (1921) who found that only 45 per cent of the summer thunderstorm precipitation falls in the daytime while Eshleman (1921) reports a figure of 39 per cent. At night the land surfaces cool very quickly in comparison to the lake which remains warmer than the land.

Not all storms of local origin, such as thunderstorms, are affected in this way. Many times, the zone of turbulence is not pronounced. This is because the temperature of the land and water surfaces are nearly equal.

The decrease in rainfall over the islands is real, although Day's theory of higher wind velocities over the gauges in the winter may account only for the lower winter precipitation. To summarize, three factors appear to operate to produce the deficiency in precipitation in the summer: (1) the effects of friction over rough and smooth surfaces, (2) the decrease in thunderstorm rainfall because the relatively cool lake water does not produce enough heat to maintain the energy of the storms, and (3) the deflection of the storms around the lake. These factors probably operate hand-in-hand to bring about a general decrease of rainfall over the lake in summer.

The annual rainfall on South Bass has varied from a high of 36.43" in 1917 to a low of 17.80" in 1934. The greatest 24-hour precipitations were 5.34" in August, 1919, and 3.50" in September, 1926.

Evaporation

Evaporation has not been measured for the islands. However, many evaporation computations have been made for Lake Erie. The estimated value of evaporation, in inches, for Lake Erie from November to April is 8.39" and precipitation is 12.81". From May to October, the evaporation has been computed at 20.90" with precipitation of 16.18". Evaporation actually exceeds precipitation. Thornthwaite (1941) and Trewartha (1943) classify the region as humid, although there is a tendency toward a prairie type of climate such as the one which existed on the adjacent mainland (Transeau 1935).

During the summer, evaporation greatly exceeds precipitation, especially in June, July, and August, being almost 5" greater. In winter and spring, precipitation is greater than evaporation.

Frost-free period

Table I gives the average length of the growing season and the average dates of the last frost in spring and the first frost in fall for Put-in-Bay and four stations 50 miles or less from the lake. South Bass Island has an average frost-free period of 205 days, while Bucyrus has an average of 154 days. North Bass, a few miles north of Put-in-Bay, has a frost-free period of 206 days (Alexander 1924). The lack of extreme temperatures between the maximum and minimum at Put-in-Bay in the spring and fall account for the long growing season as is shown in Table I. When the monthly mean temperature at Put-in-Bay is about 40°, the monthly mean minimum will be about 33°. At Bucyrus, for the same monthly mean, the mean

minimum temperature would be 29°. No other climatic factor has such a pronounced effect on the growing season.

Hudgins (1943) states that South Bass has a retarded spring. The threshold temperature of 42.8° (6.0°C) is used to denote the beginning of the blossoming period. The blossoming period is retarded in spring because of the slow warming of the lake. This retardation accounts for the slower blossoming of the flora on the island as compared to the nearby mainland. Vegetation development indicates that the temperatures are retarded even though the frost-free season is very long. Both Moseley (1899) and Core (1948) show that the spring frost-free season is exceedingly long. Moseley (1899) in accounting for the long springs says:

> "Moreover, the heat given out by the water in winter as it freezes, modifies the climate of the adjacent land. It would seem that an equal amount of heat should be absorbed by the ice melting, and thus the winter prolonged into spring, but for the region about the western end of the lake this is not true, because a great part of the ice is blown away toward the east end of the lake, whose period of cold is prolonged thereby."

However, the frost-free season is not an indication of higher average temperatures, for the springs are much cooler than on the mainland, due to the slow heating of the lake. This was apparently overlooked by both Moseley and Core. The frost-free period has varied from 169 days in 1922 to 239 days in 1931.

Fog

Fogs are rare, but they do occur during the late fall and early spring. Two types of fog prevail: advection fog, produced by warm air over cold water, and steam fog, created when cold air passes over relatively warm open water (Trewartha 1943). The average annual number of days with dense fog is 5 and partially foggy weather is found about 15 days per year (U. S. Dept. Agric. 1941, Freeman 1926).

Cities located on the north side of the lake, Port Stanley, Buffalo, and Detroit, have an average of 24.5 days with fog whereas Toledo, Cleveland, Erie, and Sandusky, which are on the south side of the lake, have an average of 16.5 days. The greater amount of fog on the north side may be explained by the fact that the warm air moving from the south produces a greater amount of fog over the lake and at the north side, leaving the southern shore generally free from fog. Steam fog is usually found in the late fall and winter, while advection fog occurs in the spring.

Winds

The prevailing wind direction throughout the year is from the southwest although there is a tendency for the wind to shift to the west and northwest during the winter months. In summer, when the temperatures are fairly high, light breezes keep the air in constant movement and there is seldom a day of oppressive heat. Periods of calm on the islands occur only occasionally during mid-summer.

In March, 1947, the wind had a sustained velocity of over 50 miles per hour for almost 24 hours, with a peak velocity of 64 miles per hour. Hutter (1952) states that the mean annual hourly speed at Toledo for a 70 year period is 11.3 miles per hour, while Put-in-Bay has 12.8 miles per hour. The flat surface of the lake permits the wind to move unobstructed over its surface thus attaining its maximum speed which is felt on the island. The higher than average wind velocities would increase the evaporation from the thin soils accounting for the semi-arid nature of the island.

Solar radiation

Figure 2 (U. S. Weather Bureau 1949) shows the annual amount of solar radiation at Put-in-Bay as compared to two mainland stations at approximately the same latitude. The higher amount of radiation at Put-in-Bay indicates clearer skies over the lake than over the land. The dip of the radiation curve in May can be explained by the fact that May is the month of heaviest rainfall and thus has a high percentage of cloudy days. The high solar radiation in June is the result of clear skies; a record which supports the theory that storms do not pass over the lake but are deflected around it. Mid-July shows another dip in the curve. In the middle of July, the water temperature and the air temperature become equal (Fig. 3) and a very stable air condition results. This condition produces haze, and the haze offers a tentative explanation for the dip in the radiation curve for July. Also to be noted is the fact that in summer, the great inequalities in heat absorption and radiation of the land mass creates strong convectional air currents. These air currents carry moisture high enough to produce towering masses of cumulus clouds over the land (rarely over the lake) and the record of solar radiation, made at land stations adjacent to the lake, is thereby affected. The cloud cover over the land reduces the amount of solar radiation received.

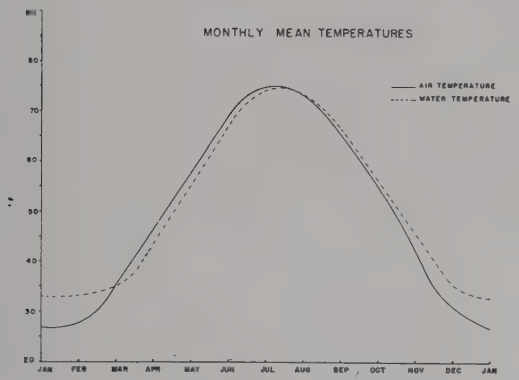


FIG. 3. Monthly mean temperature of air and water at South Bass Island.

Water temperatures

Water temperatures are taken twice daily throughout the year, at 8:00 A.M. and 4:00 P.M., by the Foreman of the Ohio State Fish Hatchery, Put-in-Bay, Ohio, at the hatchery pier. During an ice cover, the temperatures are taken at the water intake valve inside the hatchery. The average lake temperature for the year is almost the same as the average air temperature (Fig. 3). Comparison of the mean monthly averages shows that there is a lag between the air temperature and the water temperature. In spring, the average air temperature increases rapidly while the water, heating slowly, lags behind. This process continues until mid-July when the water and the air temperatures are the same. In fall, the air temperature begins to decrease more rapidly than the water and the water again lags behind, a complete reversal of the spring conditions.

Western Lake Erie is the warmest section of Lake Erie during the summer. In the summer, the deeper waters to the east are much cooler in comparison to the western basin which is continuously stirred to the bottom. The cooler water to the east probably accounts for the shorter frost-free period and the lower summer temperatures experienced at Buffalo, Erie, and Cleveland. It can clearly be seen that the shallow waters of the western basin heat rapidly in the spring and lose their heat quickly in the fall in relation to other stations in the lake.

The highest mean monthly water temperature recorded at Put-in-Bay was 78° in July, 1949. Millar (1952) shows that the average July temperature in the Western basin is 72.2°, the central basin 69.7°, and the eastern basin 68.4°.

THE MICROCLIMATES

The study of the microclimates shows the detailed changes which occur on the island. Figure 4 shows the location of the 37 temperature stations and the topography of the island.

Separating East Point from the main island is a narrow neck of "made land," a filled-in swamp, about 14 acres, where the Perry International Memorial Monument stands. East Point is relatively flat and the greatest height is not over 22

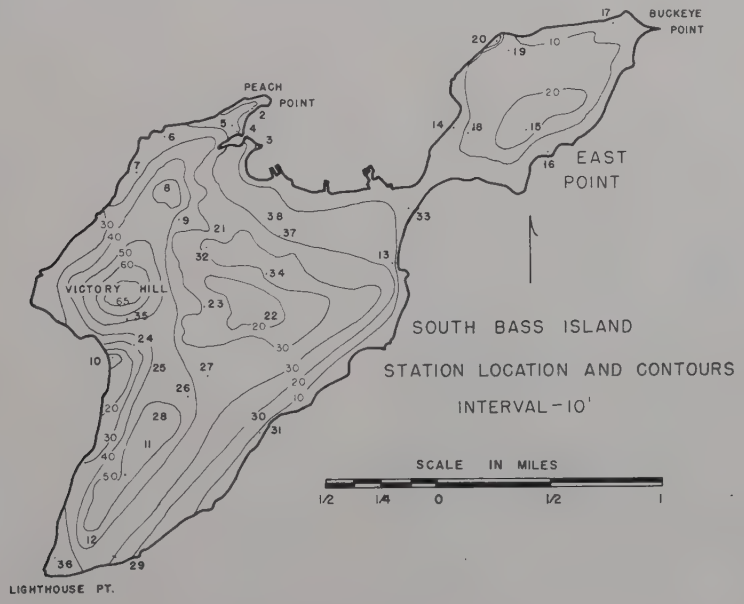


FIG. 4. Station locations and topography of South Bass Island.

feet above the lake level. The soils are chiefly Catawba loams with a small amount of Randolph stony loam. The northwest shore, in the vicinity of station 20, is rocky and ends in an abrupt cliff about 20 feet above the lake. East Point has very little forested land, less than 2.5 per cent, which is located in the vicinity of the Randolph soils. The remainder of the point is in vineyards and grains.

The main island is varied in many respects when compared to East Point. The large areas of Randolph and Rodman soils, almost ⅖ of the total acreage of the main island, are forest-covered. The Randolph soils are very thin and numerous rock outcrops make the land only suitable for pasture or woods. On the Catawba soils, the principal land-uses are grains, pastures, and vineyards. Bordering the large protected bay is the village of Put-in-Bay. The northwest shore, with the exception of the area near station 10, has steep 20-35 foot rocky cliffs. The region near station 10 is a narrow low pocket and borders on a small bay known as Stone's Cove. Lighthouse Point lies over 30 feet above the lake surface and ends in steep rocky cliffs. The entire southeast shore slopes upward in a gentle grade toward the interior of the island. This shore has rock or gravel beaches. On the interior of the island, the area near station 22 is one of the lowest and the Victory Hill section, station 35, is the highest part of the island. Changes of elevation from 5 to 9 feet are too small to be shown on the contour map. Many of these small changes in elevation are associated with the numerous caves on the island (Verber and Stansbery 1953).

Station locations

Seven distinct microclimates are recognized on the island. However, it should be pointed out that 37 microenvironments could be established from the records of the 37 temperature stations. For purposes of simplicity, the data were placed into groups from which the seven microclimates were distinguished. They fall into two broad groups, the shore microclimates and the inland microclimates.

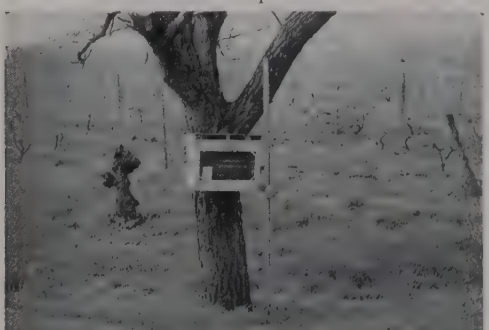


FIG. 5. High Inland Station No. 9, at typical station arrangement.

All stations were from 3.5 to 4.5 feet above the ground with the exception of station 32 which was one foot above the ground. Standard U. S. Weather Bureau thermometers and thermometer shelters were used. Periodic checks were made on all thermometers to insure standardization. Because of a few irregularities in the records, one complete year, from November 1944 to October 1945, was studied intensively for the present paper. Figure 5 shows a representative station.

Methods

The maximum and minimum temperatures at each station were read daily and the mean monthly temperatures were computed for each station. These monthly averages were placed on a map of the island and the mean isotherms were drawn. The stations were located on the island with relation to the varying topography of the island and with respect to ease in recording.

Although this study is by no means as detailed and as broad as that made by Wolfe, *et al.* (1949), it is similar in many respects. Wolfe studied the macroclimate and microclimates of a small valley in central Ohio which is comparable in area to South Bass Island. However, the topography was much more varied and rugged, having rocky cliffs over 50 feet in height and an elevation range of over 300 feet. Not all stations of Wolfe's study were checked daily, but comparisons were obtained by utilizing the weekly data. The study revealed three different types of maximum temperature regimes: stations in the open such as cliff tops and open fields, forested slopes and uplands, deep gorges and coves. Although the variations in elevation on the island were very small, significant changes in temperature were evident from one part of the island to another. Whereas Wolfe's study continuously showed great thermal variations, these were not always apparent on the island due to the stabilizing influence of the lake, yet differences of 26° were recorded during a single day.

The present study showed seven microclimates: high leeward, station 20; high windward, stations 6, 29, 36; low leeward, stations 2, 3, 4, 14, 17; low windward, stations 10, 13, 16, 31, 33; high inland, stations 9, 11, 12, 26, 28, 35; low inland, stations 15, 18, 19, 21, 23, 24, 25, 27, 30, 32, 37, 38; wooded, stations 5, 7, 8, 22, 34.

The vegetation of the high and low windward

stations consists primarily of lichens, species of *Biatorella* and *Teloschistes* which exist on the rocky cliffs as well as some of the mosses which include species of *Amblysteguim, Brachythecium, Fissidens, Grimmia, Gymnostomum, Tortella,* and *Tortula.* In the more protected leeward stations, the species of lichens such as *Dermatocarpon* and *Psora* are more conspicuous (Core 1948). The inland stations present a wide variety of vegetational associations. The abandoned vineyards and fields usually have a secondary succession of staghorn sumac (*Rhus typhina* L.) and red cedar (*Juniperus virginiana* L.). The grasses, Canada bluegrass (*Poa compressa* L.) and Kentucky bluegrass (*Poa pratensis* L.) are abundant in the dry, high inland fields and meadows. The wooded areas, as mentioned previously, are primarily hackberry and blue ash.

Habitat characteristics

Low leeward stations are located on the low (0'-20' above the lake) protected shores of the island. In the fall, the water temperature exerts a direct influence. The daily temperature range between the maximum and minimum is only a few degrees. In winter, because of its low and protected location, this range is somewhat greater than the higher shore stations. In the spring as the water again begins to warm, the range is less than at the other shore stations. In summer, the range is greater than all other stations because of its protected position. This habitat has the longest frost-free season on the island, primarily because of its proximity to the lake.

The low windward stations are those from 0' to 20' and exposed to the prevailing wind. The fall, winter, and spring daily temperature ranges, between the maximum and minimum are somewhat greater than at the low lee stations. The summer range, however, is smaller because of its exposed position. The frost-free season is less than at the low leeward stations.

The high windward and leeward stations (20' and over) are very similar in daily temperature ranges, varying only a few degrees. The windward stations usually have a greater range because of the exposed location. The extreme maximum temperatures are higher and the extreme minimum temperatures are lower for the lee stations. The frost-free periods are similar.

The low inland stations are usually well-protected. This habitat has the greatest daily range of temperature between the maximum and minimum in fall and winter than the other habitats. In spring and summer, the minimum temperatures are the lowest on the island, but the maxima are not extreme. The extreme minimum temperatures in winter have fallen to —18° when upland and shore stations were —3° and 0° respectively (Dec. 29, 1944). The frost-free season was only 187 days, some 60 days less than at the low lee stations. Air drainage and back radiation play an important part in maintaining the low minimum temperatures in this habitat.

The high inland stations are usually exposed and open in nature. The daily ranges are less than the low inland stations because of the higher minimum temperatures. The frost-free season is greater than the low inland station by more than 20 days, yet far less than at the shore or wooded area stations.

The stations located in wooded areas were both high (20' and over) and low (0-20'). The daily ranges of temperature for all seasons were between the shore and inland station temperatures. This was also true of the extreme maximum temperatures and the frost-free period. The foliage of the trees during the summer prevented extreme temperatures within the wooded areas. During the winter period, however, the extreme minimum temperatures were usually lower that at the shore stations but higher than those of low inland stations.

Hourly temperatures

Station 2, located over the lake had a thermograph, and other related weather data were recorded bi-hourly for a one-year period, from 1945 to 1946. Changes of temperature as great as 14° were recorded within two hours, but usually the variations were much smaller. On May 22, 1945, a cold front passed and within less than two hours the temperature dropped 14°. On July 28, 1945, in the late afternoon, a warm front passed over the island and the temperature increased 4° within an hour after the passing of the front. Undoubtedly, the changes of temperature would have been much greater had it not been for the influence of the lake.

Temperature inversions

Temperature inversions near the ground, 0 to 5 feet as shown by Wolfe, appear to be normal and quite common. On South Bass, two adjacent stations were located in a low pocket, one a foot above the ground and the other at 3.5 feet. The average for 213 recorded inversions was 2.4°F in 2.5 feet. Over a 300 day period, there were 213 days on which an inversion occurred, or 71 per cent. Over this period, there were 14 days when no inversion occurred and 73 days when the temperatures were equal. One difference of 8° in 2.5 feet occurred during this period.

Daily temperatures

The greatest changes in temperature occurred during the day. In the winter, the lake temperature was 33°, very close to the freezing point. The shore stations were still under the influence of the lake whose temperature was much higher than the air temperature. The shore stations had a much smaller range of temperature and a higher average temperature than the inland stations. The temperatures of the wooded areas were between those of the shore and open inland stations. The low frost pocket dropped to —8° whereas the high lee stations were as much as 10.5° above zero. The average temperature of the inland stations reflect the much lower temperatures that occur away from the lake. The maximum temperatures were very similar for all stations.

In spring, there were very few variations in the daily temperatures around the island. The high inland stations recorded the highest maximum temperature and the low inland stations the lowest temperature. As a rule the inland stations showed a greater range of temperature and higher average temperatures. The higher average temperatures in spring for the inland stations were somewhat greater because the shore stations were retarded by the lower lake temperatures.

In summer the low leeward shore stations, being protected from the prevailing winds usually had the highest temperatures. The open inland stations were second to the lee shore stations. The lowest temperatures occurred in the low inland areas where back radiation was at a maximum. The smallest range of temperature and the lowest average temperature were in the wooded areas. The lower portion of the forests is open while the canopy is very dense, keeping out the direct sunlight. The open nature of the woods allows a free circulation of air. The greatest range of temperature was at the low shore stations which had unusually high maximum temperatures.

The changes in fall are somewhat similar to the spring temperatures. The highest maxima and lowest minima were inland. The high lake temperatures insulated the shore stations during the night and thus the range was usually from 3° to 6°. The inland stations, with maximum heating and cooling had ranges of 8° to 14.5°. The wooded regions were again between the shore and inland temperatures. In fall, the lake temperatures lag well behind the air temperatures, thus the shore stations have higher temperatures than the inland stations, opposite of the spring period.

Frost-free season

The frost-free season varies markedly on South Bass Island. In 1945, the low inland stations had a variation in the frost-free period from 187 to 191 days, the high inland stations from 190 to 213 days and the wooded stations from 215 to 236 days. The shore stations all had over 235 days frost-free with the low lee stations varying from 235 to 251 days depending upon the exposure of the site.

Air drainage does not appear to be a factor in the frost-free variations because of the small differences in elevation. However, cool clear nights in both fall and spring favor high rates of back radiation from the inland stations.

The range of the frost-free season at South Bass Island for the various parts or habitats of the island was 187 to 251 days in 1945. The season varied as much as 64 days when comparing one habitat to another. The variation on the island exceeds the normal range that occurs between Bucyrus and Put-in-Bay. The average difference for the two stations being about 15 days. No doubt selected habitats near the vicinity of Bucyrus would also show changes as large as those that occur on South Bass Island.

Monthly temperatures

Isothermal maps of the island were constructed from the average monthly temperatures. The average monthly temperature is not as striking as the daily changes that occur; however different parts of the island show distinct changes of temperature during the late fall, winter, and early spring. This is the period of high winds. During the summer period, the low (less than 22 feet) flat land of East Point shows the greatest changes in temperature and is the hottest part of the island. The temperatures increase toward Buckeye Point which has the lowest elevation and is surrounded by water on three sides. The region of Stone's Cove, station 10, is on the windward side of the island and much lower temperatures prevail. The low pocket is flanked by 25- to 30-foot cliffs on two sides and a sharp hill at its back. During the period of southwest winds in late fall and winter this pocket is one of the coldest areas on the island. The gently sloping southeast shore is also cool in the early spring. The prevailing southwest winds move inland along the unobstructed shore and thus keep this region cooler than most parts of the island. During the spring when the lake is cooler than the air, the temperature is noticeably reduced on the exposed windward coasts. The rocky Peach Point area which is both leeward and windward is surround-

ed by water on three sides and is directly influenced by the lake. In the spring, it is cooler than the adjacent inland area and in fall it is somewhat warmer.

In November, the protected inland stations and the lee shore stations have the highest temperatures. The low southeast coast is the coolest with a long arm of lower temperatures moving toward the interior of the island. During December, the more protected regions, both inland and coastal have the higher temperatures, the low exposed pocket at Stone's Cove being the coolest part of the island. The lowest mean temperatures occurred in January, from 17° to 19°. The lake was frozen and thus the higher water temperatures under the ice had no effect on the shore stations. The more protected and leeward areas were still the warmest and the low southeast shore the coolest. The lake was still frozen in February (Fig. 5) and the southeast shore had a pattern very similar to January. The warmest part of the island was in the protected northeast part of the main island. East Point had very uniform temperatures and was almost isothermal. With the gradual warming of the air temperatures in March and the breaking of the ice, the low shore stations had lower temperatures, retarded by the cooler lake temperatures. The northwest shore which is 25 to 30 feet above the lake showed little or no effect from the lower lake temperatures and was the warmest part of the island. April showed very little change. The coolest region was windward and the warmer areas in the lee of the island. The low region of Terwillegar's Pond, near Peach Point, was cooler than the areas next to it, probably the influence of the lower lake temperature. East Point was still isothermal. The month of May showed the first characteristic change in the preceding pattern. The entire island was within one degree of being uniform. A small inland section of East Point was somewhat warmer than the rest of the island. The former trend of the isotherms was usually northeast-southwest, during May the change was to the northwest-southeast. In June (Fig. 6), the northwest-southeast trend of the isotherms was more evident and the prevailing wind was from the southeast. A wedge of lower temperatures appeared to be injected through the low central portion of the island. Isolated forested areas and the low tip of East Point were the warmest parts of the island. East Point had temperatures from 72° to 74° while the main island varied from 70° to 72°. In August, the wind was south and the wedge of lower temperature through the central area of 71° to 75° was still present. East Point with temperatures from 73° to 75° was the warmest part of the island. September, much like May, was nearly isothermal. The great changes that occurred in June, July and August were no longer evident. During the preceding summer months the wind velocity ranged from 6.9 to 10.5 miles per hour.

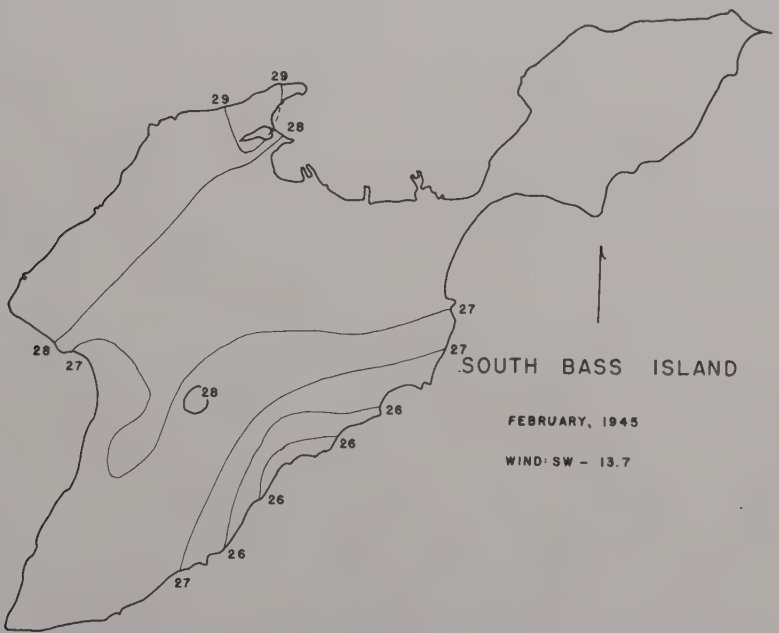


Fig. 6. Isotherms for February, 1945, representing a typical winter month.

By September, the average wind velocity had increased to 12.7 miles per hour. The northwest-southeast trend of the isotherms is not as clear as the previous months, but it is still detectable. By October the southwest-northeast trend is clear once again and the low protected areas, such as Peach Point had the highest temperatures. The interior regions were now cooler than the lee shore stations.

The distribution of isotherms on South Bass Island brings out certain patterns of temperature. The location of the station in relation to lee or windward exposure and high or low altitude appears to be an important factor. A station may be windward for most of one month and be leeward the next. This may change the entire temperature pattern of the station. The average wind velocity appears to control the range of temperature on the island. During the period when the winds are from 12.0 to 14.9 miles per hour the range on the island is from 1 to 3 degrees. In the summer when the wind velocity is less than 11 miles per hour, the range is 4 to 5 degrees. The trend of isotherms seems to be governed by the prevailing wind direction. On the island, the trend was parallel to the direction of the wind.

Annual extremes

In 1944, the highest temperature ever recorded on the island 107.5°, was recorded on the low lee station of East Point. From 1945 through 1948, the inland stations, with the exception of the forested areas, had the prevailing high temperatures. The dates of the maximum temperatures at different stations varied as much as one month. The extreme minimum temperatures were always recorded in the low inland pockets, —18°, with the wooded areas second. The high windward stations had the highest minimum temperatures, probably tempered somewhat by the lake. The yearly range of temperatures in 1944 was 125.5°.

Summary

Several points can be drawn from the foregoing study about the climate of the island and the effects of the lake. The lake acting as a great heat reservoir exerts a stabilizing influence on the areas nearby.

South Bass Island has a small daily range of temperature compared to nearby interior mainland stations due to the tempering effect of the lake. The mean summer and fall temperaturatures are high while the winter and spring temperatures are lower than the nearby mainland stations.

The annual precipitation is noticeably less than the adjacent mainland stations. The decrease in summer rainfall is produced by the small number of thunderstorms over the lake. Not only do thunderstorms seems to be deflected around the lake as is implied by the high solar radiation rate, but also the storms that do cross the lake do not produce much rain. The exceedingly high temperatures over the land can maintain the energy needed to stimulate a thunderstorm, but they are not found over the lake which is much cooler.

South Bass and the other islands have the longest frost-free periods (at their margins) in the entire state of Ohio, even though they are the most northern part of the State. The high heat capacity of the lake prolongs the summer temperatures far into the fall while the small range of temperature between the maximum and minimum daily temperatures permits a long spring. The long frost-free period however does not indicate a long growing season. The spring temperatures are retarded and the threshold temperatures occur much later on the island than on the mainland.

The amount of potential evaporation on the island is greater than the precipitation. This high rate is most pronounced in the summer months. The rate of evaporation may account for the drought-hardy species of trees that are found on the island.

Solar radiation at Put-in-Bay is greater than other stations at the same latitude in the east-central United States. Two prominent dips occur, one in May when the island receives its maximum precipitation and one in late July. During late July, the air temperature and the water temperature are the same and this condition produces a great amount of haze over the lake. This haze reduces the amount of solar radiation received on the island.

The western basin of Lake Erie is the warmest large body of water in the Great Lakes. This great heat reservoir reduces the range of temperature and modifies the climate of the adjacent regions.

South Bass Island, about 2 square miles, was sampled by 37 temperature stations from July, 1944, to August, 1948, for the study of the microclimates of the island. Seven microclimates were apparent: high and low leeward shore stations, high and low windward shores, high and low inland stations, and wooded areas.

Daily temperatures showed the most significant changes. In winter, the variations between the low frost pockets and high lee shore stations were as great as 18°. During the summer, the lee shore stations, especially the East Point area, were the warmest parts of the island. In fall, the range

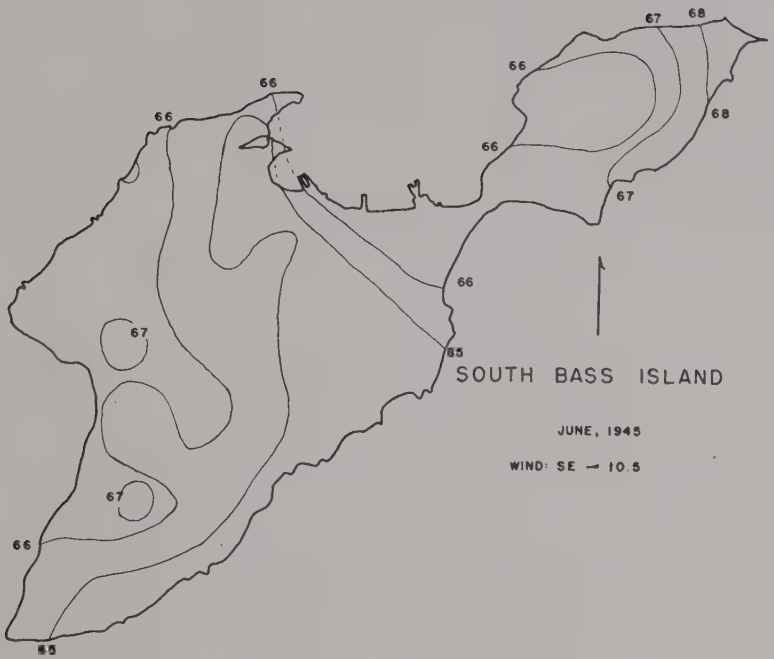


FIG. 7. Isotherms for June, 1945, representing a typical summer month.

of temperature of the shore stations was from 3 to 6 degrees whereas inland stations varied from 8 to 14 degrees. The higher temperatures of the lake appear to insolate the shore stations against sudden cooling and heating.

The frost-free season of the island varied in 1945 from 187 to 251 days for various selected habitats. The range on the island is greater than that which normally occurs between South Bass Island and Bucyrus.

Monthly temperatures at Put-in-Bay show two distinct trends of the isotherms. During the period of southwest winds, the isotherms are parallel to the island and this shifts to the northwest-southeast during the south and southeast winds. In the late fall, winter and spring the warmest parts of the island are the lee shore stations and the protected inland stations. In summer, East Point was the warmest part of the island. In May and September, the months previous to the shift in isotherms, the island was almost isothermal.

REFERENCES

Alexander, W. H. 1924. A climatological history of Ohio. Ohio State Univ. Eng. Exp. Sta. **28**: 1-175. Bull. **26.**

Day, P. C. 1926. Precipitation in the drainage area of the Great Lakes, 1875-1924. Monthly Weather Rev. **54**: 85-106.

Core, E. L. 1948. The flora of the Erie Islands. Ohio State Univ., F. T. Stone Lab. Contrib. No. **9.** 106 p.

Eshleman C. H. 1921. Do the Great Lakes diminish rainfall in the crop growing season? Monthly Weather Rev. **49**: 500-503.

Freeman, J. R. 1926. Regulation of elevation and discharge of the Great Lakes. The Sanitary District of Chicago, Ill. 548 p.

Horton, R. E., and C. E. Grunsky. 1927. Hydrology of the Great Lakes. A report to the Chicago Sanitary District. Chicago. 432 p.

Hudgins, B. 1943. The South Bass Island community. Econ. Geog. **19**: 16-36.

Humphreys, W. J. 1921. On the difference between summer daytime and night time precipitation in the United States. Monthly Weather Rev. **49**: 350-351.

Hutter, H. K. 1952. Eighty years of weather and climate at Toledo, Ohio. Ohio Jour. Sci. **52**: 62-75.

Leighly, J. 1941. Effects of the Great Lakes on the annual march of air temperature in their vicinity. Papers Mich. Acad. Sci. **27**: 377-414.

Millar, F. G. 1952. Surface temperatures of the Great Lakes. Jour. Fisheries Res. Bd. Canada **9**: 329-376.

Moseley, L. 1899. Sandusky Flora. Ohio Acad. Sci., Sp. Papers No. **1.**

Thornthwaite, C. W. 1941. Atlas of climatic types in the United States 1900-1939. U. S. Dept. Agric. Misc. Pub. **421.** Washington, D. C. 95 p.

Transeau, E. N. 1935. The prairie peninsula. Ecology **16**: 423-437.

Trewartha, G. T. 1943. An introduction to weather and climate. McGraw-Hill Book Co., New York. 545 p.

U. S. Dept. of Agric. 1941. Climate and man. U. S. Dept. Agric. Yearbook. Washington, D. C. 1064 p.

———. 1949. Trees. U. S. Dept. Agric. Yearbook. Washington, D. C. 944 p.

U. S. Weather Bureau. 1949. Weekly mean values of daily total solar and sky radiation. U. S. Dept. Commerce Tech. Paper No. 11, Washington, D. C. 17 p.

Verber, James L., and David S. Stansbery. 1953. The caves of South Bass Island. Ohio Jour. Sci. **53**: 326.

Wolfe, John N., R. I. Wareham, and H. T. Schofield. 1949. The microclimates of Neotoma, a small valley in central Ohio. Ohio State Univ. Studies **8**: 1-267. Ohio Biol. Surv. Bull. **41**.

STUDIES ON MOISTURE RELATIONSHIPS IN EARTHWORMS[1]

WILLIAM C. GRANT, JR.
Department of Zoology, Dartmouth College, Hanover, New Hampshire

A megascolecid earthworm, *Pheretima hupeiensis,* indigenous to the Chinese mainland, occurs as a peregrine form in the eastern United States. Chen (1933) has given the first verified report of the finding of the species in America from a specimen collected at Philadelphia. Spreading rapidly through the medium of turf transplants by 1948 the worm appeared in epidemic proportions on golf greens in Westchester County, New York and Fairfield County, Connecticut.

A comprehensive study of the biology of the species was initiated in 1951. Its morphology was re-examined with special reference to size and weight (Grant 1955 *in press*) and experiments were undertaken in the laboratory to determine its tolerance to desiccation and temperature. A final study dealt with observations made on *P. hupeiensis* in the field.

Earthworms normally live in moist soils where the atmosphere is always near or at saturation. However, they may be subjected to periods of drought and in agricultural lands are frequently turned out of the soil and exposed to surface conditions. It is at such times that the vital limit of desiccation and rate of water loss become of importance to a species. Earthworms of various species studied by Schmidt and Stchepkina (1917), Schmidt (1918) and Hall (1922) contained about 83 per cent water with respect to body weight. The percentage of water in different portions of the body wall of *Pheretima* (sub *Perichaeta*) *divergens* and *megascolidiodes* is described by Hatai (1924). Jackson (1926) gives values from 87.3 to 88.8 per cent for the water content of the common earthworm *Lumbricus terrestris.* Schmidt records that a specimen of *Eisenia foetida* lost 61.6 per cent of its body weight and recovered when placed on a moist surface, while Hall revived a specimen of *Allolobophora* which had lost 69.6 of its body weight. The loss of water by worms under conditions of desiccation has not been thoroughly investigated. Overton (1904) states that a single worm examined lost weight in direct proportion to the time elapsed, but Jackson believes that the rate decreases with time. Morrison (1946) calculated the rate of water loss in mgs./gm./min. for earthworms of an unidentified species. However, as these worms were not desiccated to uniform end-points, his results are difficult to interpret. Wolf (1938) described a "dehydration syndrome" for *Lumbricus terrestris,* and studied the efficiency of worms in reaching the peripheries of circular fields of different dehydrating capacity. Michon (1949) has shown that when *Allolobophora caliginosa* were kept in soil which had been slowly dried in the laboratory, they went into a state of diapause, enclosed in earth capsules lined with a mucus secretion. When kept in moist soil, the worms remained active for eighteen months. A survey of the earthworm populations of Ohio conducted by Olson (1928) showed that the greatest numbers of worms occurred in soils containing from 12 to 35 per cent moisture.

The present investigation has been concerned with the determination of the percentage water content, vital limit of desiccation and rates of desiccation of *P. hupeiensis* and the reaction of the animal to environments of different dehydration capacity. In order to make the interpretation of results more meaningful, two common lumbricid worms *Allolobophora calignosa* and *Eisenia foetida* have been used throughout in comparative studies.

The author wishes to express his appreciation to Dr. Roger B. Friend, Dr. Grace E. Pickford, and Professor G. Evelyn Hutchinson for their advice and aid during the course of the investigation. Funds contributed under a grant by the Westchester-Connecticut Turf Improvement Association financed research during the summer

[1] This study represents Part II of a dissertation submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at Yale University, New Haven, Connecticut.

of 1952 at The Connecticut Agriculture Experiment Station.

Methods

In the following experiments all specimens of *P. hupeiensis* were obtained from the greens nursery plot of the Pelham Country Club, Pelham, New York. Specimens of *E. foetida* were collected in compost at the experimental farm of The Connecticut Agriculture Experiment Station in Hamden, Connecticut and *A. caliginosa* were obtained from the grounds of Yale University and private property in Hamden.

Before the experiments the worms were kept on moist cheesecloth for four or five days, during which time they evacuated their gut contents. Previous to desiccation the worms were reduced to basal weight by rolling them on blotting paper several times according to the procedure of Wolf (1940) in order to remove excess surface moisture and any water stored in the gut or nephridia. Animals were stored and experiments performed at 20.5°C.

In order to determine the precentage water content, worms were weighed on an analytical balance accurate to 0.1 mg. before being placed in an oven at 110°C. where they were dried to a constant weight.

In determining the vital limits of desiccation experimental animals were reduced to basal weight, weighed and placed on a wire mesh grid over 10 grams of anhydrous calcium chloride in a large weighing bottle. It was found necessary to place a piece of filter paper over the grid in order that contact with the metal would not cause the animals to react by secreting excess coelomic fluid through the dorsal pores.

Immature and mature worms of the three species were weighed and placed in the desiccator described above. The time for individuals to reach a percentage loss in body weight approximating values already estimated for desiccation tolerance was recorded.

A circular field thirty-five inches in diameter was constructed of large sheets of blotting paper upon which four concentric zones were mapped. These zones were four inches in width, allowing for a central zone three inches in diameter. In each case 11 worms were placed in the central zone and the time was recorded for 6 individuals to reach the periphery of the field. A similar series of experiments was conducted after the field had been thoroughly soaked with conditioned tap-water. It is a well known fact that earthworms are sensitive to light as described by Hess (1924) for *Lumbricus terrestris* and by Howell (1939) for *Pheretima agrestris*. However, Walton (1927) showed that worms are insensitive to red light and Bretnall (1927) confirmed these results. Consequently the above experiments were conducted under a red light to assure greater accuracy of the results.

The soil moisture preference of worms was studied in a cylinder 6 inches in diameter and 24 inches high constructed of 1-mm. mesh wire. Its base was placed in a battery jar and the column filled with sandy loam. The entire column was then soaked with water, and a water table two inches deep was allowed to form in the bottom of the jar. Worms were placed in the soil and after a period of two weeks the 0-6, 6-12, 12-18 and 18-24 inch levels of the column were removed and the number of specimens in each zone counted. The moisture content of a large sample of soil from each zone was determined. The loss of water in an oven at 110°C was calculated as a percentage of the oven dry weight of the soil as is customary in such determinations.

Observations and Results

Water Content

The results of this experiment are given in Table I. The body water of *P. hupeiensis* accounts for 82.3 per cent of its body weight, when the animal is kept in saturated air on moist cheesecloth. *A. caliginosa* contains 85.0 per cent water and *E. foetida* contains 84.1 per cent under the same conditions. The values for *E. foetida* were recalculated from data given by Schmidt (1918).

Table I. *Percentage of water content*

Species	Number	Mean percentage water
Pheretima hupeiensis.....	18	82.3±1.18†
Allolobophora caliginosa....	12	85.0±1.26
Eisenia foetida*.....	13	84.1±3.61

*Data recalculated from Schmidt (1918).
†Standard deviation.

It should be noted that according to Adolph (1927) worms kept on moist surfaces are not completely hydrated. However, the above figures represent the water content in the body tissues of worms under natural moisture conditions, after having been reduced to basal weight and their gut evacuated of soil. There was no difference in the water content of immature and mature worms of *P. hupeiensis* and *A. caliginosa*. Although Schmidt did not indicate the maturity of his worms, it is probable they were mature because of their large size. The water content of three immature worms of *E. foetida* determined in the present studies was 83.9 per cent, in close agreement with Schmidt's values.

Vital Limits of Desiccation

It is important to know the maximum loss in body weight an animal can sustain and be expected to recover. It is to be expected that some individuals of a population can sustain a greater loss of body water than others. Consequently, the true vital limit of desiccation cannot be defined by extreme cases, but should rather represent a mean value for the water loss which 50 per cent of the population can be expected to endure. In calculating such a mean it is important that numbers of animals be subjected to approximately the same degree of desiccation, the latter being estimated from pilot experimentation to fall near the vital limit of desiccation for a species.

In the present investigations numerous pilot experiments were run on each species to be studied. *P. hupeiensis, E. foetida* and *A. caliginosa* have a characteristic appearance when they approach their vital limit of desiccation. It was therefore possible to judge the proximity of individuals to the bological end-point under consideration. At this stage in *P. hupeiensis* the entire surface is dark and dry with small droplets of coelomic fluid appearing in the region of the dorsal pores. The caudal end is greatly shrunken, while the anterior segments before the clitellum appear swollen. As *E. foetida* approaches its vital limit of desiccation the body forms a smooth curvature with the opposing ends in contact. The surface appears dark and dry, but shrinkage of the posterior portions is not so pronounced as in *P. hupeiensis*. In *A. caliginosa* the body surface is moister than in *E. foetida,* and the curvature is less pronounced.

During desiccation worms normally leak coelomic fluid from the dorsal pores, which flows slowly over the body. In the present experiments, when the flow of coelomic fluid was greatly increased, stains appeared on the surface of the filter paper in the desiccators. All specimens showing such activity were discarded, as in these cases weight loss could not have been accounted for by water alone, but would have included solid elements of the coelomic fluid.

When the data had been assembled the percentage loss in body weight of each specimen was plotted against its original body weight. The weights of individuals which died following desiccation and those which survived were plotted in separate columns. Horizontal lines were then drawn through the point representing the greatest loss in body weight sustained by an individual which survived, and that representing the minimum loss of weight which caused death. The mean percentage loss in body weight was then calculated for all points falling between the lines. This mean is taken as an approximation of the vital limits of desiccation for a given species (Fig. 1). These values in terms of percentage loss of body weight and total body water are given in Table II. It is clear from Figure 1 that maturity had no noticeable effect on the vital limits of desiccation.

TABLE II. *Vital limits of desiccation*

Species	Number	% loss body weight	% loss body water
Pheretima hupeiensis....	12	48.6±0.45*	59.2
Allolobophora caliginosa.	32	63.4±1.64	74.7
Eisenia foetida.....	24	58.8±1.47	70.0

*Standard deviation.

Time to the Vital Limits of Dessication

The time for immature and mature individuals of different sizes to reach their respective vital limits of desiccation was taken for a number of worms of all three species. Under the standard conditions of these experiments this time may be taken as a measure of the rate of desiccation which is a function both of the size of the worm and the properties of its body surface. The relationship between body size and time to the vital limit of desiccation in shown graphically in Figure 2. Inspection of the curves showed that in each species there is a definite "break" in the relationship at the time of sexual maturation. Taking the initial body weight as the independent variable the regression coefficient for mature and immature specimens of each species was calculated according to the allometric growth equation $y = bx^k$, and the values of k, which may be termed the dehydration coefficient, are given in Table III. The time to the vital limit of desiccation is determined not only by this constant but also by the initial value of the intercept (b). The correlation coefficients (r) are highly significant.

The immature specimens of each species differ in their relationships. The time to the vital limit

TABLE III. *Time to the vital limit of desiccation**

Species	Category	N	b	k	r
P. hupeiensis	Immature	10	3.3	0.63	0.99
	Mature	10	14.1	0.23	0.90
A. caliginosa	Immature	7	13.8	0.33	0.87
	Mature	12	15.3	0.14	0.95
E. foetida	Immature	7	1.2	0.94	0.95
	Mature	10	12.6	0.41	0.98

*Calculated from equation $y=bx^k$, where x is initial body weight; y time to the vital limit of desiccation; k the dehydration coefficient.

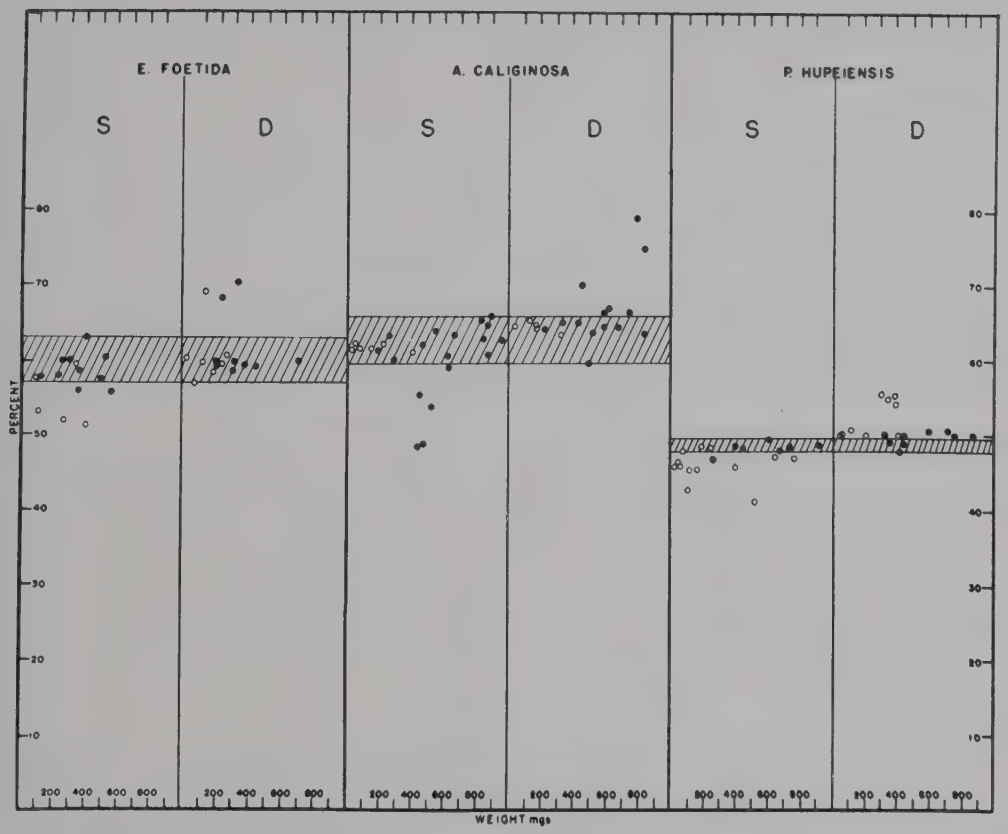


FIG. 1. The vital limits of desiccation of *E. foetida, A. caliginosa* and *P. hupeiensis*. The percentage loss of body weight is plotted against intitial body weight. The mean loss of body weight for all points falling within the shaded area for a given species is taken as its vital limit of desiccation. Open dots indicate immature and solid dots mature animals.

of desiccation in respect to body size increases fastest in *E. foetida* and slowest in *A. caliginosa,* with *P. hupeiensis* having intermediate values. However, as a result of the high value of the intercept (b) for the young of *A. caliginosa,* they take a longer time to reach an end-point than the other species, and maintain this advantage relationship throughout although possessing a lower dehydration coefficient. This may be interpreted to mean that the rate of evaporation is superimposed on a more resistant mechanism to dehydration.

The adults of each species lose water at a faster rate relative to body weight than immatures. Approximately the same relationship between the species is maintained in the adults as in the immature. The ratios of the dehydration coefficients $\left(\frac{k \text{ immature}}{k \text{ mature}}\right)$ are 43.7, 36.5, and 42.5 for *E. foetida, P. hupeiensis* and *A. caliginosa* respectively.

Effect of Surfaces of Different Dehydrating Capacity on the Activity of Worms

Dry Field. Worms were placed in the center zone of the dry field of blotting paper. Eleven worms were used in each experiment in a series of three experiments for each species, two being conducted on mature and one on immature individuals. The time for six worms, or 54.5 per cent of the population to reach the periphery of the field was recorded, and has been termed the relative escape time.

The relative escape times for three experiments with *P. hupeiensis* were extremely close, averaging about 12 minutes. *E. foetida* had an average escape time of 11.3 minutes. The zonal distribution of this species was noted at the end of 12 minutes for comparison with that of *P. hupeiensis* for the same time period. Experiments on *A. caliginosa* yielded strikingly different results. Combining the total of all three experiments per-

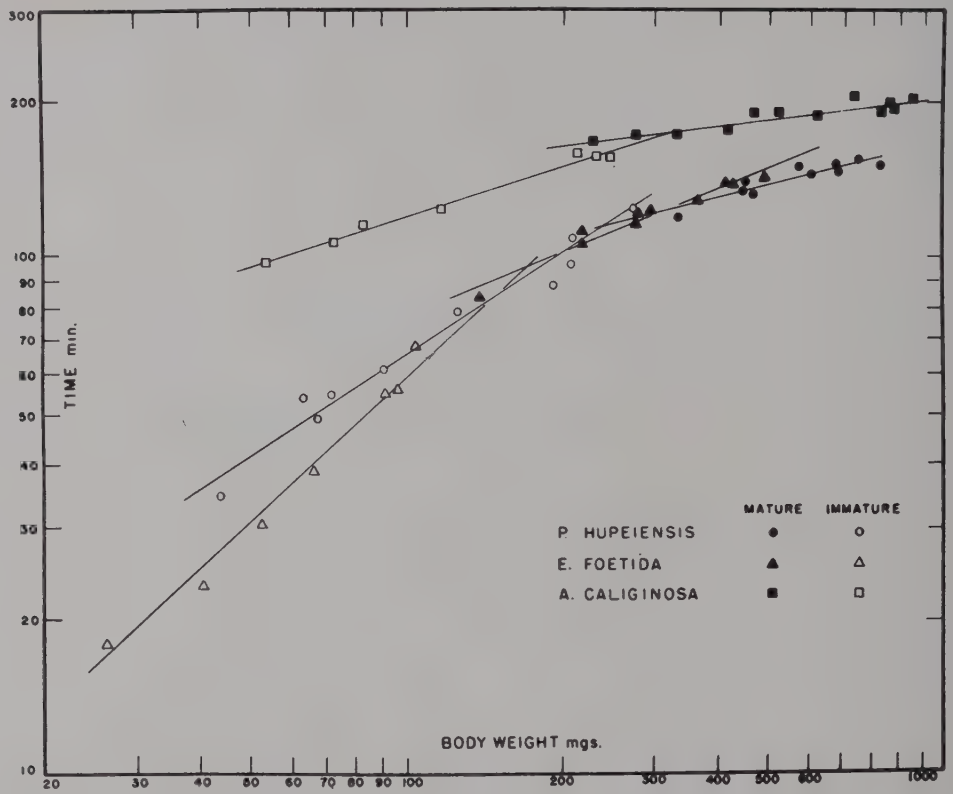


FIG. 2. The relation between initial body weight and time for individuals of *P. hupeiensis, A. caliginosa* and *E. foetida* to reach their vital limit of desiccation.

formed on the species, only two individuals had reached the periphery of the field in 12 minutes, and twenty-six still remained in the central zone. Experiments were extended to 40 minutes until it was evident that little further activity could be expected, but the worms still remained in the central zone. Within this area the worms did quite a bit of probing, and were covered with a mucous-like secretation from the dorsal pores.

Wet Field. In these experiments the field was soaked with water. It is interesting to note here that worms kept on such a surface for several days showed no apparent signs of desiccation though exposed to relative humidities of about 69 per cent.

When specimens of *P. hupeiensis* were placed on the wet field they migrated to the peripheral regions immediately. The escape time for the three experiments was 3.5 minutes. The experiment was continued for 12 minutes in order to get a comparative zonal distribution with that of the dry field. The escape time of *E. foetida* was 4.5 minutes. The zonal distribution was recorded at 3.5 and 12 minutes for comparison with *P. hupeiensis* at those times. In the case of *A. caliginosa,* no individuals reached the periphery of the field and thirty-one remained in the central zone. It was felt that mutual thigmotaxis as described by Smith (1902) might be effective in keeping the worms localized, but single worms placed on wet paper showed no more inclination to migrate than when numbers were present. The ratios of the relative escape times for *P. hupeiensis* on the dry and wet field were 1 :3.4, and 1 :2.5 for *E. foetida.* Figure 3 gives the zonal distribution on the dry field after 12 minutes and on the wet field after 3.5 and 12 minutes for each species. It should be noted that this figure represents the combined results of three experiments each on the wet and dry fields. A study of a large number of desiccating worms showed that dehydration syndromes could be described for each species. Immature worms are inactive in the later stages of desiccation and secrete little co-

elomic fluid although they are quite active in the initial phases as indicated by their escape times which correspond closely to those of mature individuals.

Soil Moisture Preference

In each of the two experiments conducted, 15 individuals of *P. hupeiensis* and 15 of *A. caliginosa* were used. The soil moisture and the distribution of the worms was recorded from the 0-6, 6-12, 12-18 and 18-22 inch levels after a period of two weeks from the time of introduction of the test animals into the experimental column. The moisture gradients established for the two experiments closely resembled each other. The percentage of soil moisture based on oven-dry weight averaged 14.5, 19.2, 27.9 and 30.1 per cent at the four levels respectively. In the first experiment 66.6 per cent of the P. *hupeiensis* were taken from the 18-22 inch level where the moisture percentage was 30.4, and in the second 80.0 per cent of the individuals were recorded from the same level at a moisture percentage of 29.9. In neither of the tests were worms found above the 12-inch level, where moisture was 18 per cent or under. No specimens of *A. caliginosa* were taken above the 12 inch level, but they did not show so marked a preference for soils of 27.9 and 30.1 per cent moisture as did *P. hupeiensis*. In the first experiment 40 per cent of the animals were in the 18-22 inch zone, and in the second 53.3 per cent. A few worms of each species that were placed in air dry soil became desiccated within a few hours. However, *A. caliginosa* can resist desiccation in slowly drying soil if it has time to encapsulate in the manner described by Michon (1949).

Discussion

The above determinations with respect to water content are in close agreement with those of other workers. This suggests that the body tissues of earthworms contain about the same amount of water, although slight variations are to be expected in the general range of 82-88 per cent.

If the figures obtained by Schmidt and Hall for *E. foetida* and *A. chlorotica* and those given by Jackson for *L. terrestris* are compared with the values presented above, it appears that lumbricid worms can be expected to sustain a water loss of at least 50 per cent of their initial body weight. It is probable that the vital limit of desiccation, calculated by Hall from a single specimen of *A. chlorotica* as being 69 per cent, represents a maximum figure and that the mean end-point for the species may fall considerably below this value. There are no determinations available for desiccation limits on any species of *Pheretima* other than *P. hupeiensis,* but the vital limit of desiccation of this species at 58 per cent suggests that the resistance of the genus may fall within the range given for lumbricid worms. As *L. terrestris* and *P. hupeiensis* contain about the same amount of body water as species whose vital limits of desiccation are higher, it seems doubtful whether there is any relationship between the percentage of water contained by the body and resistance to desiccation. It should be noted that the low temperatures used by Schmidt and Hall to extend survival time in desiccated individuals, while of interest, are of little biological significance, as a worm desiccated at high surface temperatures cannot be expected to escape to soil regions of 1-10°C to recover. As little agriculture or gardening is conducted during the winter months in temperate regions, it is probable that animals exposed on the surface of soils must usually endure dehydration at spring and summer temperatures of 20°C or more.

Adult *E. foetida, A. caliginosa* and *P. hupeiensis* dehydrate at a faster rate than the immature individuals. The reason for this is their greater activity and discharge of coelomic fluid from the dorsal pores during desiccation as shown by the study of dehydration syndromes. It is to the advantage of a worm to keep its surface moist, as it remains not only more active and thus able to escape harmful environmental conditions, but through rapid evaporation from its integument can regulate its body temperature acording to the wet-bulb principle described by Hogben and Kirk (1944). However, the loss of coelomic fluid is only an initial advantage, as the integument is moistened at the expense of internal body water. Though adult worms are not so efficient in maintaining water as the immature, they are capable of burrowing back to moist soil levels within a short time following surface exposure. Despite their lower rate of desiccation, immature worms appear to be less efficient in escaping surface conditions as they are less active during the later stages of desiccation. Dimo (1938) has indicated that in the very arid regions where moisture frequently falls to the hygroscopic coefficient, the greatest mortality is sustained by juvenile members of a worm population. It would be of extreme interest to know the mortality rates for adults and young worms in areas recently subjected to ploughing.

As mentioned previously, though *A. caliginosa* has a faster rate of evaporation it has an initial mechanism more resistant to desiccation than *E. foetida* or *P. hupeiensis*. Young and mature

worms of *A. caliginosa* differ only slightly in their reaction to dehydration, as is reflected in the fact that the difference in dehydration coefficients between the two categories is small. *A. caliginosa* is quite inactive when exposed to dehydration. In dry and wet experimental fields large numbers of individuals remained within the central zone, while *P. hupeiensis* and *E. foetida* migrated rapidly to the periphery. The reaction of *A. caliginosa* is appropriate for an animal that frequently encapsulates in dry soils rather than retreating to moister levels. The inactivity and secretion of mucous substances on the dry field may actually represent the initiation of a diapause reaction. On the other hand, *P. hupeiensis* and *E. foetida* are not known to go into diapause, and presumably evade unfavorable environmental circumstances by moving away from them. It should be pointed out that *A. caliginosa*, despite an apparent diapause mechanism, is unable to ward off eventual desiccation in air dry soils. It is possible that true anabiosis may exist in some earthworms, though this phenomenon has not been described for any of the earthworms of humid zones.

In the moisture-preference studies *P. hupeiensis* and *A. caliginosa* both chose soil levels where the percentage moisture was well above the hygroscopic moisture range, preferring regions where soil moisture is from 20 to 30 per cent. In air-dry soils both species became desiccated within a few hours. As the water present in such soils can be assumed to be largely hygroscopic, it seems probable that such bound water is as unavailable to earthworms as it is to plants.

Summary

Moisture relationships have been studied in two species of common lumbricid earthworms, *Allolobophora, caliginosa* and *Eisenia foetida,* and in the megascolecid worm *Pheretima hupeiensis.* The water content expressed as a percentage of the initial body weight is about the same for all three species, with a range from 82 to 85 per cent.

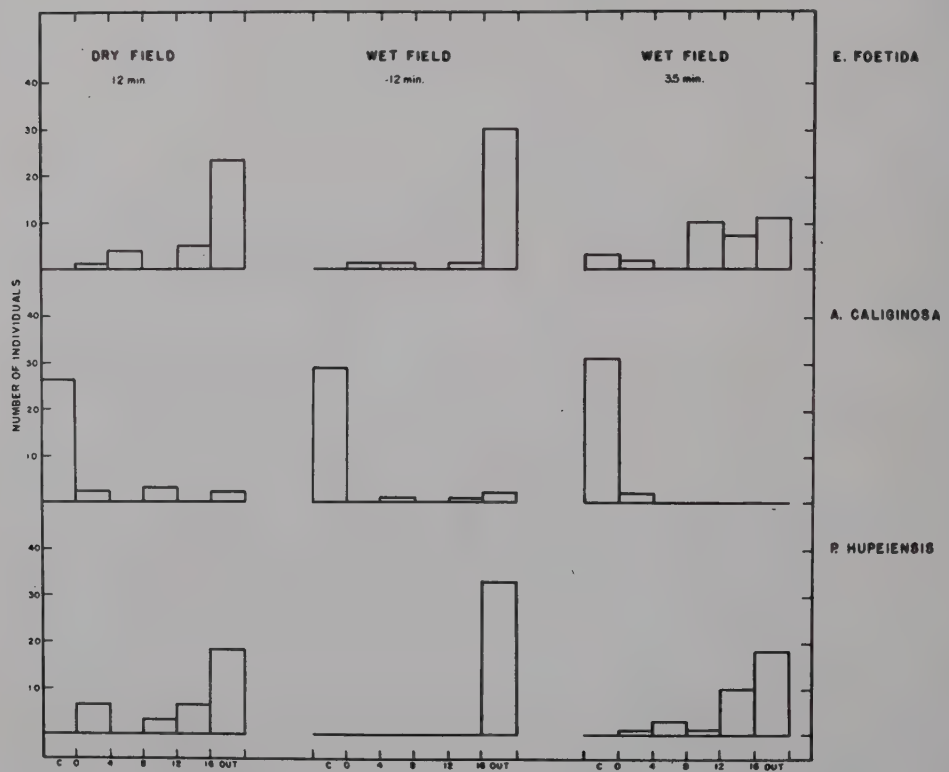


Fig. 3. Activity of *E. foetida, A. caliginosa* and *P. hupeiensis* on fields of different dehydrating capacity. The zonal distribution of individuals of each species is given at the end of 12 minutes on the dry field and at the end of 3.5 and 12 minutes on the wet field.

Their vital limits of desiccation have been determined. *P. hupeiensis* is able to withstand a 48.6 per cent loss of body weight, but *E. foetida* and *A. caliginosa* can sustain losses up to 58.8 and 63.5 per cent respectively. The time for worms of the above species to reach their vital limits of desiccation has been recorded. *A. caliginosa* appears to have a more efficient mechanism for resisting desiccation than the other two species. Mature and semi-mature worms of each species desiccate more rapidly than do immatures. This is counterbalanced, however, by the fact that in nature the adults are better equipped to return to moist soil levels after exposure to dehydration at the surface. In studying the activity of the worms on surfaces of different dehydrating capacity, *P. hupeiensis* and *E. foetida* are found to be more active on a wet than on a dry field. *A. caliginosa* is relatively inactive on both surfaces, and may have begun the initiation of a diapause reaction by the secretion of mucus in unusual amounts. In a moisture gradient in a soil column *P. hupeiensis* and *A. caliginosa* both chose regions well above the hygroscopic moisture level. In general the results indicate that *P. hupeiensis* and *E. foetida* must depend on a relatively moist environment, and that *A. caliginosa,* while unable to tolerate extreme moisture deficiencies, has a wider range of tolerance concomitant with its ability to go into diapause under certain conditions.

References

Adolph, E. F. 1927. Regulation of volume and concentration in the body fluids of earthworms. J. exp. Zool., **47**: 31-62.

Bretnall, G. H. 1927. Earthworms and spectral colors. Science, **66**: 27.

Chen, Y. 1933. A preliminary survey of the earthworms of the lower Yangtze Valley. Contr. biol. Lab. Sci. Soc. China, **9**: 177-296.

Dimo, N. A. 1938. Earthworms in the soils of Central Asia (in Russian) Pedology, **4**: 494-526.

Grant, W. C. 1955. An anatomical study of the peregrine megascolecid earthworm Pheretima hupeiensis in the eastern United States. Proc. U. S. Nat. Mus. In press.

Hall, F. G. 1922. The vital limit of desiccation of certain animals. Biol. Bull. Woods Hole, **42**: 31-51.

Hatai, S. 1924. Observations made on Megascolidiodes on the relation of body length to the number of segments and setae. Sci. Rep. Tohoku Univ. (4) **1**: 23-38.

Hess, W. N. 1924. Reactions to light in earthworm Lumbricus terrestris. J. Morph., **39**: 515-542.

Hogben, L. and R. L. Kirk. 1944. Studies on temperature regulation I. The Pulmonata and Oligochaeta. Proc. roy. Soc., **132B**: 239-252.

Howell, C. D. 1939. The response to light of the earthworm *Pheretima agrestris* with special reference to the function of the nervous system. J. exp. Zool., **81**: 231-259.

Jackson, C. M. 1926. Storage of water in various parts of the earthworm at different stages of desiccation. Proc. Soc. exp. Biol., **23**: 500.

Michon, J. 1949. Influence de la desiccation sur la diapause de lombricien. C. R. Acad. Sci. Paris, **228**: 1455.

Morrison, P. R. 1946. Physiological observations on water loss and oxygen consumption in Peripatus. Biol. Bull. Woods Hole, **91**: 181-188.

Olson, H. W. 1928. The earthworms of Ohio. Ohio Biol. Surv. Bull, **17**: 47-90.

Overton, E. 1904. Neunundreissig Thesen uber die Wasserökonomie der Amphibien und die osmotischen Eigenschaften der Amphibienhaut. Verh. phys-med. Ges. Wurzburg, **26**: 277-295.

Schmidt, P. 1918. Anabiosis of the earthworm. J. exp. Zool., **27**: 55-72.

———, and T. Stchepkina. 1917. Sur l'anabiose des vers de terre. C. R. Soc. Biol. Paris, **1919**: 366-368.

Smith, A. C. 1902. The influence of temperatures, odors, light and contract on the movements of the earthworm. Amer. J. Physiol., **6**: 459-486.

Walton, W. R. 1927. Earthworms and light. Science, **66**: 132.

Wolf, A. V. 1938. Studies on the behavior of *Lumbricis terrestris* L. to dehydration and evidence for a dehydration tropism. Ecology, **19**: 233-242.

Wolf, A. V. 1940. Paths of water exchange in the earthworm. Physiol. Zool., **13**: 294-308.

NATURAL REVEGETATION ON A FIELD ABANDONED FOR THIRTY-THREE YEARS IN CENTRAL KANSAS

G. W. Tomanek, F. W. Albertson, and Andrew Riegel

Department of Botany, Fort Hays Kansas State College, Hays, Kansas

Introduction

In 1920, an 80-acre field located on a gentle slope in the college pasture near Hays, Kansas, was retired from cultivation and fenced into a native pasture. The soil was typical of this type of site. The soil profile about midway down the slope was poorly developed with an indistinct horizon varying from 2 to 12 inches (5.1 to 30.5 cm.) in depth. It was typically dark brown in color and granular in structure but was intermixed with scattered pieces of distintegrating Fort Hays limestone. Below 12 inches (30.5 cm.), the soil was distinctly yellow in color with an increasing amount of fragmented rock. Total depth varied from 6 inches (15.2 cm.) on the upper slope to over 6 feet (1.8 m.) on the lower slope. This

FIG. 1. Heavy growth of sand dropseed outside and inside exclosure after 22 years of succession.

kind of site is usually clothed with a mixture of mid-grasses which are generally more prevalent on the shallow soil while short grasses occupy the deeper ones on the upland.

In 1932, an experimental exclosure was built in this area. Since that time successive changes in the vegetation have been recorded. Riegel (1944) outlined 4 stages of secondary succession from bare cultivated soil to climax. The area had passed through the annual weed stage, short-lived perennial grass and forb stage (Fig. 1), and at the time of his study, it was in the third stage where the long-lived perennial grasses were found among the less stable perennial grasses and forbs. The fourth stage would be the climax condition.

The study was understaken to determine two things: (1) what degree of climax had been attained after 33 years of succession, and (2), what was the effect of moderate grazing on the rate of succession. Over 400 square-foot samples were taken to determine variations in cover and species composition of the vegetation. This method has been described in detail by Voigt and Weaver (1951). Half the samples were inside the exclosure and half outside to determine the effect of grazing on composition of the vegetation. Four hundred samples were also taken on nearby lightly grazed areas in order to make comparisons with the subsere studies. Even though the effect of light and moderate grazing probably held these areas slightly below climax, for convenience they

TABLE I. *Per cent composition of each grass species at different stages of secondary succession and per cent of climax furnished by each species*

Species	Climax on similar site	After 23 yrs. succession without grazing		After 33 yrs. succession without grazing		After 33 yrs. succession with grazing	
		Per cent composition	Per cent climax	Per cent composition	Per cent climax	Per cent composition	Per cent climax
Buffalo grass	16.5	73.3	16.5	21.0	16.5	61.3	16.5
Blue grama	26.8	6.6	6.6	11.3	11.3	2.7	2.7
Side-oats grama	35.2	....	....	8.7	8.7	2.4	2.4
Big bluestem	4.8	....	....	1.8	1.8	....	....
Little bluestem	2.2	....	....	1.6	1.6	....	....
Western wheatgrass	9.5	....	....	8.2	8.2	1.2	1.2
Hooker's dropseed	T	....	....	4.0	T	....	....
Three-awn grasses	5.0	0.3	0.3	20.1	5.0	19.9	5.0
Sand dropseed	T	19.8	....	20.7	T	9.4	....
Silver beardgrass	....	....	....	1.0	....	0.5	....
Windmill grass	....	....	....	1.6	....	2.6	....
Total	100.0	100.0	23.4	100.0	53.1	100.0	27.8
Basal cover	39.4	36.3	....	32.8	....	52.3	....

will be referred to as climax areas in this paper.

Nomenclature of grasses encountered in this study follows Hitchcock and Chase (1950).

Composition

Recovery of important species of grass involved in succession on this site is shown in Table I. Comparisons were made between climax normally found on this site, and degree of recovery attained after 23 years of succession (Riegel 1944), 33 years of succession with protection, and 33 years with moderate grazing.

Early in succession, buffalo grass (*Buchloë dactyloides*) was one of the first long-lived perennial grasses to occupy the area and, because of rapidly growing stolons, it soon furnished the major portion of the plant cover (Fig. 2). After 23 years of succession, Riegel (1944) found that it furnished nearly three-fourths of the cover but now, 10 years later, with the increase of other climax grasses, it comprised only 21 per cent of the vegetation (Table I). When subjected to moderate grazing outside the exclosure, buffalo grass had become even more important. The large amount of leaf area close to the ground enables this grass to be extremely resistant to grazing (Branson 1953). Therefore, it furnished nearly two-thirds of the vegetative cover at the expense of grasses less tolerant to grazing.

Side-oats grama (*Bouteloua curtipendula*), normally the most important grass in the climax on this type of site (35.2 per cent), had made its initial appearance in the last 10 years of succession and now comprised 8.7 per cent of the vegetative cover. It was not so plentiful on the grazed as on the protected area.

Blue grama (*Bouteloua gracilis*) is one of the 3 dominant grasses in the climax on this type of site, but it comprised only 11.3 per cent of the cover at this point in the succession. It had, however, nearly doubled its cover in the last 10 years. Recovery of this grass to its former abundance was retarded by moderate grazing. Even after 33 years of recovery, when grazed it had considerably less cover than it did after only 23 years of protection.

Big bluestem (*Andropogon gerardi*) and little bluestem (*Andropogon scoparius*) were found in small amounts only on areas protected from grazing. These highly preferred grasses had not gained a foothold in utilized areas. Although not very abundant in the climax of this site, they serve as excellent indicators of the last stage of succession.

Western wheatgrass (*Agropyron smithii*) was found growing in almost pure stands scattered over the area on soils that were deeper and heavier textured than average for this site. After 33 years of development, it had almost reached (8.2 per cent) its abundance found on climax areas (9.4 per cent) but under moderate grazing it was much less plentiful (1.2 per cent).

Sand dropseed (*Sporobolus cryptandrus*) is usually found in disturbed areas. It is one of the first perennial plants to occupy an abandoned field and helps to stabilize the habitat until it is replaced by longer-lived perennials. Relative abundance of this grass fluctuates greatly with seasonal climatic variations, but it still comprised nearly one-fourth the vegetation after 33 years of succession on the protected location. However, it was much less abundant on the area that had been grazed.

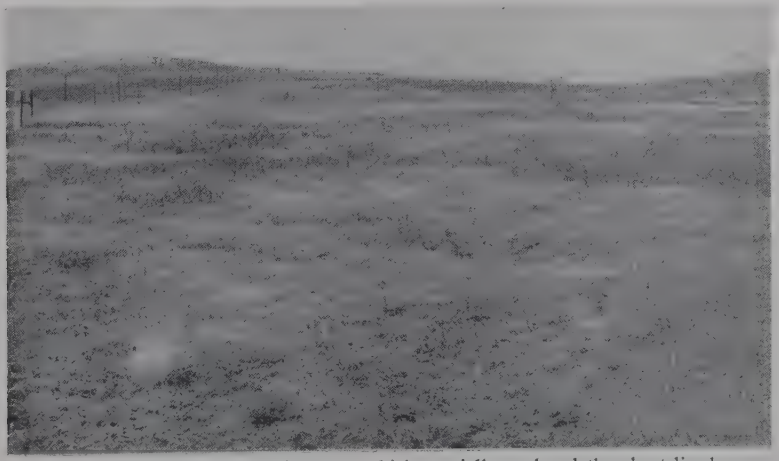


Fig. 2. Appearance of buffalo grass which partially replaced the short-lived grasses after 26 years of succession. Note higher percentage of buffalo grass outside exclosure.

Two three-awn grasses (*Aristida purpurea*) and (*A. longiseta*) are normally found in small amounts under climax conditions. Like sand dropseed they are among the early short-lived perennials that invade a disturbed area and often serve as good indicators of past disturbance. They still furnished 20 per cent of the cover after 33 years of succession on both the protected and grazed locations (Table I). The relatively low percentage composition found by Riegel (1944) is probably due to the seven-year drought (1933 to 1939) immediately preceeding his study since these grasses are very sensitive to dry weather.

Hooker's dropseed (*Sporobolus asper* var. *hookeri*) comprised 4 per cent of the total vegetation under protection even though it is found only in traces under climax conditions. It is generally a common grass on lowland but is seldom found on this site.

Two invaders, windmill grass (*Chloris verticillata*) and silver beardgrass (*Andropogon saccharoides*), were still found in measurable amounts. Traces of other short-lived perennial grasses such as Texas crabgrass (*Schedonnardus paniculatus*) and squirrel-tail (*Sitanion hystrix*) were also found. In favorable years, the two annuals, little barley (*Hordeum pusillum*) and downy chess (*Bromus tectorum*), were numerous.

Cover

There seemed to be very little difference between basal cover of vegetation on the climax and protected areas undergoing succession for 23 or 33 years. However, it was considerably greater under moderate grazing (Table I).

Per Cent of Climax Composition

Although 65 per cent of the cover on the protected area and 75 per cent on the grazed area was composed of climax grasses, it cannot be assumed that these areas are that near climax condition. Certain grasses, such as buffalo grass, are much more plentiful during succession than when climax is reached. In classifying range condition, Dyksterhuis (1949) determined the per cent of climax represented by the composition of vegetation. In this study, a similar method was used to determine the per cent of climax composition attained by the areas undergoing secondary succession. The figures given in Table I show the per cent of total vegetation furnished by each species. Some species have not yet reached the abundance they maintain under climax conditions, some are about the same, and others are even more abundant in this stage of secondary succession. In determining the per cent of climax attained, the amount given to each species cannot exceed the portion it furnished in the climax. Total climax percentage was determined, therefore, by adding percentages furnished by each climax species. Thus, after 23 years, the protected area had attained only 23 per cent of climax even though it was well-covered with grass, 80 per cent of which were climax grasses (Table I).

During the next 10 favorable years of high rainfall, the area protected from grazing reached 53 per cent of climax. However, under moderate grazing, succession did not progress as rapidly (27.8 per cent). Buffalo grass was still in greatest abundance and only small amounts of the other climax dominants had succeeded in becoming established. Most of the grasses grew in pure stands rather than in the intimate mixtures characteristic of climax grassland.

Discussion

Clements (1928) has described succession as the movement of populations and waves of invasion which rise and fall until climax is reached. Many studies have been made on the developmental stages that occur on abandoned crop land. However, very few studies have reported the length of time necessary for these subseres to reach climax from the initial stage. In western North Dakota, Whitman *et al.*, (1943) had records of areas which had been abandoned for 40 years but had not yet reached climax. They estimated it would take from 40 to 60 years to reach climax in that area. Booth (1941), working in east-central Oklahoma and southwestern Kansas, found 4 stages of development: (1) weed stage, (2) annual grass, (3) bunch grass, and (4) fully developed prairie. After 30 years, the areas were still in the bunch grass stage and did not appear to be nearing the fully developed prairie. The weed stage lasted 2 years and the annual grass stage 9 to 13 years. Weaver and Albertson (1944), studying the recovery on mixed prairie in west-central Kansas following the drought, classified the stages of the subsere as: (1) early weed, (2) late weed, (3) early native grass, and (4) late native grass. Savage and Runyon (1937) found that even after 40 years none of the abandoned fields of the southern Great Plains possessed a cover comparable in composition with the climax or subclimax of the region. However, they did find that some fields reached an optimum stand of the better species after 25 years of succession. Weaver (1954), working in true prairie, found that, in 13 years of protection following the great drought, an old degenerated pasture approximated a dynamic equilibrium not unlike the adjacent climax.

Riegel (1944), working on the area used in this study, found that nearly 80 per cent of the cover was composed of climax grasses after 23 years. However, working on the basis previously discussed, it had reached only 23.4 per cent of climax. The rapid increase of buffalo grass following the great drought (1933 to 1939) accounted for the high percentage of climax grasses and the low percentage of climax composition.

Length of time necessary for vegetation on this site to reach climax is still not known. The low figure of 53.1 per cent of climax composition after 33 years of recovery was probably due in part to the effects of the drought. During the 7-year dry period, succession probably proceeded at a slow rate if, indeed, it was not replaced by regression. However, droughts are common in the Great Plains and should be considered as part of the climatic limitations to recovery.

Vegetation on this site after 33 years of development was composed of both long-lived and short-lived perennial grasses. During the last 10 years, the short-lived and many long-lived grasses previously nonexistent or relatively unimportant, have increased on areas formerly occupied by buffalo grass.

Buffalo grass has played a major role in the development of the subsere for the last 22 years (Fig. 3). Gradual increases in cover of this species during the drought, and very rapid spread following the drought (1940-1947), were phenomenal. However, in the last few mesic years (1947-1953) the rather solid cover of buffalo grass has become interspersed with other grasses. Bare areas began to appear in the shortgrass cover and permitted the invasion of short-lived species like the three-awn grasses and sand dropseed. Large areas were also occupied by side-oats grama. It is possible that, in the absence of grazing, excess mulch hampered the growth and rooting of buffalo grass stolons and thus helped to cause the formation of these bare areas. The mulch layer under protection was more than twice as thick (3 to 9 cm. deep) as it was in the grazed area, consequently, buffalo grass was much more abundant on the grazed area. Even though much of its area had been invaded by other species, buffalo grass was still more plentiful in this subsere than it was in the climax. Side-oats grama had not yet reached its climax abundance.

Summary

A grassland area which had been abandoned from cultivation was studied to determine the per cent of climax composition attained after 33 years of recovery and the effect of moderate grazing on the rate of secondary succession.

The site was located on a gentle slope with an immature soil varying in depth from a few inches on the upper slope to over 6 feet on the lower one. The near-climax vegetation for the same kind of site was found to be a mixture of mid- and short-grasses.

After 33 years of recovery under protection, the

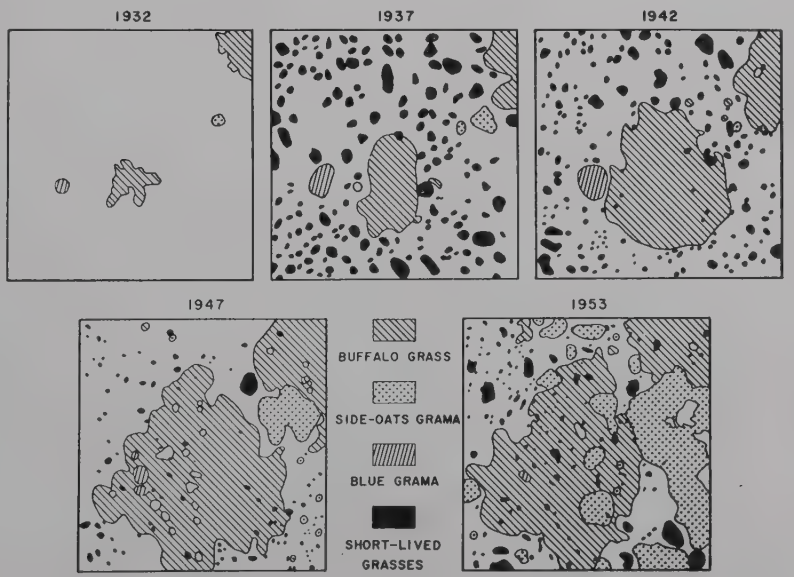


Fig. 3. Charted vegetation on a 16 square meter area showing succession at various stages during the last 20 years. The short-lived grasses were not charted in 1932.

vegetation had a basal cover of 32.8 per cent. It was composed of 55.6 per cent long-lived and 44.1 per cent short-lived perennials. The grazed area had only 32.8 per cent short-lived species and the rest were long-lived. The principal long-lived species under grazing was buffalo grass which helped to account for the higher basal cover (52.3 per cent).

The protected area had attained 53.1 per cent of climax composition while the grazed location had only 27.8 per cent. Comparisons were made with a previous study by Riegel (1944) on the same area after 23 years of recovery.

References

Booth, W. E. 1941. Revegetation of abandoned fields in Kansas and Oklahoma. Amer. Jour. Bot. **28**: 415-422.

Branson, Farrel A. 1953. New factors affecting resistance of grasses to grazing. Jour. Range Mgt. **6**: 165-171.

Clements, F. E. 1928. Plant succession and indicators. H. W. Wilson Co., New York.

Dyksterhuis, E. J. 1949. Condition and management of range land based on quantitative ecology. Jour. Range Mgt. **2**: 104-115.

Hitchcock, A. S., and Agnes Chase. 1950. Manual of the grasses of the United States. U. S. Dept. Agr. Misc. Pub. **200** (rev.). 1051 p.

Riegel, D. A. 1944. A comparative study of natural and artificial revegetation of land retired from cultivation at Hays, Kansas. Kans. Acad. Sci. **47**: 195-214.

Savage, D. A., and H. Everett Runyon. 1937. Natural revegetation of abandoned farm land in the central and southern Great Plains. International Grassland Congress. Aberystwyth, Great Britain, Rept. Sect. 1 (Grassland Ecology): 178-182.

Voigt, J .W., and J. E. Weaver. 1951. Range condition classes of native midwestern pasture: An ecological analysis. Ecological Monog. **21**: 39-60.

Weaver, J. E. 1954. A seventeen-year study of plant succession in prairie. Amer. Jour. Bot. **41**: 31-38.

Weaver, J. E., and F. W. Albertson. 1944. Nature and degree of recovery of grassland from the great drought of 1933 to 1940. Ecological Monog. **14**: 393-479.

Whitman, Warren C., H. Theo. Hanson, and Gordon Loder. 1943. Natural revegetation of abandoned fields in western North Dakota. North Dakota Agr. Exp. Sta. Bull. **321**: 18.

TEMPERATURE RELATIONSHIPS IN THE MEGASCOLECID EARTHWORM *PHERETIMA HUPEIENSIS*[1]

WILLIAM C. GRANT, JR.
Department of Zoology, Dartmouth College, Hanover, New Hampshire

The earthworm *Pheretima hupeiensis* is indigenous to the Chinese mainland, but occurs as a peregrine form on golf greens in the eastern United States. A re-examination of the anatomy of the species and a study of its moisture relationships together with those of two lumbricid worms, *Eisenia foetida* and *Allolobophora caliginosa,* has been reported by Grant (1955a, 1955b). The present paper deals with experiments conducted in the laboratory on the temperature relationships of the species. Where practical *E. foetida* and *A. caliginosa* were used in comparative studies.

Temperature is one of the most important conditions to be considered in the environment of an animal. In accordance with the classification of Fry (1947), temperature may destroy the integrity of the organism, initiate a directive response or have effects upon metabolism. Poikilothermic animals, whose body temperature tends to approximate that of their immediate surroundings, can be expected to sustain a rapid loss or gain of heat in accordance with shifts in environmental temperature. Rogers and Lewis (1914, 1916) measured the body temperatures in the earthworm *Lumbricus terrestris* (sub Agricola) submerged in water. They demonstrated that the worms come into equilibrium with environmental temperatures in about two minutes with an accurracy of 0.05° after a change of 10°C. Hogben and Kirk (1944) measured the body temperatures of *L. terrestris* under varying conditions of temperature and relative humidity. Like terrestrial gastropods the earthworm can maintain a lower body temperature than that of its surroundings by evaporation of body water. When the air was "comparatively moist" at relative humidities above 37 per cent the body temperatures were not greater than 2°C above that of a wet-bulb thermometer. However, at a relative humidity of 18 per cent or lower, the worms were less efficient in maintaining low body temperatures due to the fact that they became desiccated rapidly. Wolf (1938) has described some lethal effects of temperature on *L. terrestris.* Worms that were submerged for

[1] This study represents Part III of a dissertation submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at Yale University, New Haven, Connecticut.

400 minutes at 29°C failed to recover when placed at 10°C. At 28.5°C only 50 per cent recovered. In another series of experiments, animals were exposed to high temperatures and their survival time was recorded. Most worms exposed for 400 minutes at 27.5°-28.5° did not survive. The thermal death point of the same species was investigated by Hogben and Kirk (1944). In moisture-saturated air worms survived for a 12-hour period at 28°C, but died during the same time interval at 30°C, the upper lethal level under these conditions being estimated at 29°C. Worms immersed at 2°C survived for at least an hour, and could be kept indefinitely in melting ice. Schmidt (1918) reported that *Eisenia foetida* failed to recover after exposure to temperatures between 1.6°C and 2.0°C. Hopp and Linder (1947) have indicated that in unprotected agricultural soils unidentified species of earthworms died when temperatures fell to 32°F. McLeese (1950) found that lobsters acclimatized at 24°C showed 50 per cent mortality when exposed to temperatures of 31°C. However, when conditioned at 5°C their upper lethal limit was about 25.5°C.

Smith (1902) studied temperature as a directive factor in *Eisenia* (sub *Allolobophora*) *foetida*. Worms placed on a heated glass plate did not react to temperatures below 28°C, but retreated immediately at 29°-35°C. Wolf (1938) placed specimens of *L. terrestris* in glass tubes, which were submerged in a water bath. At 27.5°C the animals showed a "thermotropic" response by crawling to the cooler end of the tubes. In a soil column immersed at 27.5°C the animals became restless and appeared frequently at the surface. Budington (1902) noted that at temperatures above 20°C a slow relaxation occurred in the muscles of *L. terrestris*.

The following experiments were concerned with the temperature preferenda and upper lethal levels of *P. hupeiensis, E. foetida* and *A. caliginosa* and the effect and rates of conditioning in *P. hupeiensis*. The author wishes to express his deep appreciation to Dr. Grace E. Pickford and Dr. Roger B. Friend for their constant interest and encouragement during the entire course of the present investigation, and to Professor G. Evelyn Hutchinson for his advice and commentary. Facilities were made available by Osborn Zoological Laboratory, the Bingham Oceanographic Laboratory of Yale University and The Connecticut Agriculture Experiment Station. A portion of the work was sustained by a grant from Westchester-Connecticut Turf Improvement Association.

Methods

For the study of preferred temperatures a soil chamber 24 inches in length, 8 inches wide and 3/8 inch in depth was constructed of glass plates held apart at the borders by strips of wood, and secured in position by Hoffman clamps. Lines were drawn across the top plate at 4-inch intervals along its length, serving to partition the chamber visually into six zones of equal area. These zones were labeled from A to F. Two 250-watt heaters were placed beneath the chamber at zones E and F, and the entire apparatus was placed in a cold room at 1-3°C. The application of the heating elements established a thermal gradient from about 75°C to 0.8°C within 45 minutes. With slight variations set up by convection currents, the initial gradient was maintained throughout each experiment. Due to the adjustment of the heating elements it was impossible to reproduce exactly the same gradient in each case, although the same general temperature range was represented.

In the study of thermal death points and the effects of acclimatization air chambers consisting of large screw-top jars were immersed in water baths accurate to 0.1°C. The air within the chamber was kept at saturation, by passing it through a catch bottle submerged in the bath. Providing the water level in the bath was not allowed to drop, thus exposing the sides of the chambers, temperatures within were constant and generally approximated that of the water within about 0.5°C. In the chambers the experimental animals were kept in flat plastic containers provided with large apertures covered with a fine bolting silk in order to allow for proper air circulation. Determinations were made in saturated air as not only does this approximate the condition of the atmosphere of most soils but also because submergence in water causes osmotic changes which could have affected the results.

Temperature Preferendum

P. hupeiensis, E. foetida and *A. caliginosa* were used in the following determinations, two experiments of thirty worms each being conducted on each species. Worms conditioned at 20°C for a month were placed at either end of the soil chamber and their distribution noted at the end of 24 hours with respect to the thermal gradient. Temperatures were recorded at the boundaries of each of the five zones (*i.e.* at the 0, 4, 8, 12, 16 and 20-inch positions).

The frequency distribution of the three species at the end of 24 hours and the temperature gradients are given in Figure 1. The experiments on *E. foetida* and *A. caliginosa* were conducted in

the same chamber. A majority of the specimens of *P. hupeiensis* congregated between 15°C and 23°C and those of *E. foetida* between 15.7°C and 23.2°C. *A caliginosa* had a wider preferendum extending between 10°C and 23.2°C. All species tended to avoid temperatures above 23°C and below 10°C though retreat from the extremes was less pronounced in *A. caliginosa*. It should be noted that the above figures represent the average of two tests, and that worms frequently passed into less favorable zones for short periods of time.

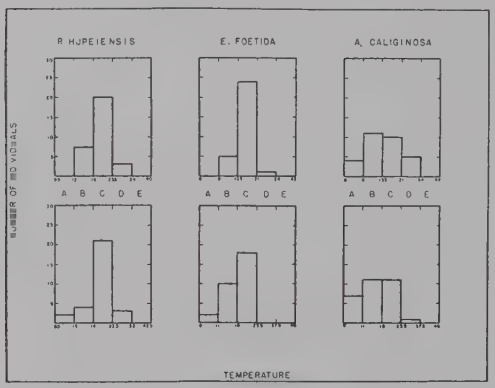


FIG. 1. Temperature preferendum of *P. hupeiensis, E. foetida* and *A. caliginosa* conditioned at 20°C.

In the above experiments worms placed initially at the warm end of the field retreated immediately as soil temperatures reached 30°C or above. This is in close agreement with the findings of Smith for *E. foetida*, which retreated at temperatures between 29°-35°C. It may be that Wolf's (1938) failure to observe any directive factor operating at low temperatures was due to the shortness of exposure time, and the fact that his worms did not show response to heat below 27°C can be explained by the fact that the animals were in glass tubes where "thermo-tropic" responses had to nullify a strong thigmotactic reaction.

Upper Lethal Temperatures

P. hupeiensis, E. foetida and *A. caliginosa* conditioned for a month at 22°C were placed at various test temperatures in a submerged air chamber and their percentage mortality recorded at each temperature over a period of 48 hours. The upper lethal temperature was defined as that temperature which could be expected to cause 50 per cent mortality of test populations in 48 hours. This particular value was adopted as it is in agreement with those used by McLeese on lobsters. Under the conditions of the experiment the upper lethal temperature can be estimated at 24.9°, 24.7° and 26.3°C for *P. hupeiensis, E. foetida* and *A. caliginosa* respectively by simple interpolation of the data presented in Table I. These results are in near agreement with those of Wolf (1938) who found that for periods of 400 minutes all worms of *Lumbricus terrestris* died when exposed to temperatures of about 29°C but that 50 per cent survived at 28°C. It is likely that had Wolf's experiments been continued for 48 hours, the apparent lethal level would have been lowered several degrees at last.

TABLE I. *Upper lethal temperatures of worms conditioned at 22°C. Nine worms were used at each test temperature*

Species	Test temperature	Per cent mortality in hours						
		1	3	6	10	23	29	48
P. hupeiensis	27.5	0	0	0	0	100	....	....
	25.6	0	0	0	0	33.3	44.4	100
	24.8	0	0	0	0	0	0	22.2
	23.7	0	0	0	0	0	0	0
E. foetida	30.0	0	0	55.5	100	....	....	....
	27.5	0	0	0	11.1	77.7	100	....
	25.6	0	0	0	0	0	22.2	100
	24.6	0	0	0	0	0	11.1	44.4
	24.0	0	0	0	0	0	0	0
A. caliginosa	27.5	0	0	0	0	0	0	100
	27.1	0	0	0	0	0	11.1	100
	26.3	0	0	0	0	0	0	55.5
	25.6	0	0	0	0	0	0	0

Acclimatization

The effect of acclimatization at different temperatures upon the upper lethal temperature of *P. hupeiensis* was investigated. Specimens were kept at 4°, 9° and 15°C for a month, thus allowing time for the individuals to become thoroughly conditioned to the environmental temperatures. Thermal death points were then determined for animals at each of the conditioning temperatures in the same manner as for those kept at 22°C. The upper lethal temperatures and temperatures at which 100 per cent survival and mortality was recorded in 48 hours are plotted against conditioning temperatures in Figure 2. In *P. hupeiensis* there is an average gain in heat tolerance of 0.3° C for every 1°C increase in conditioning temperature. However, at temperatures above 25°C these effects can be expected to be less pronounced as the conditioning temperature approaches the absolute limits of thermal tolerance.

Because of technical difficulties little investigation was conducted at lower lethal levels. At 3°C *E. foetida* died within 5 days, while *P. hupeiensis* lived for about a week. However, *A. caliginosa* survived and remained active for several weeks. At 0°C *P. hupeiensis* conditioned

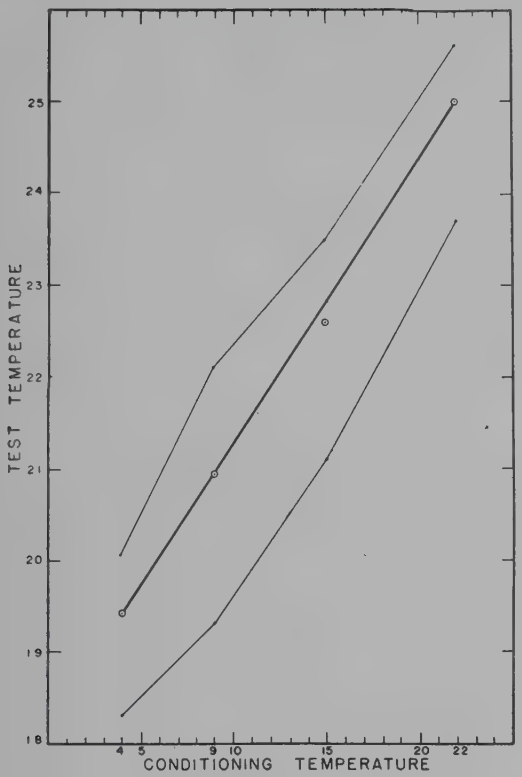


FIG. 2. Effect of conditioning at different temperatures on the upper lethal temperature of *P. hupeiensis*. Open circles represent temperatures at which 50 per cent mortality occurred within 48 hours. Solid points represent extremes of 0 and 100 per cent mortality in 48 hours.

at 22°C died within 48 hours, while a few specimens of *E. foetida* survived for 55 hours. It is not likely that earthworms can sustain temperatures much below the freezing point regardless of the acclimatization factor. This is emphasized by the deaths of worms in unprotected soils at 32°F as recorded by Hopp and Linder (1947).

RATE OF THERMAL ACCLIMATIZATION

Specimens of *P. hupeiensis* kept at 15°C for a month were placed in soil at 22°C. Six worms were removed on the 1, 2, 4, 6, 10, 12, 14, 16 and 18th days of exposure to the new environment and placed in an air chamber at 24.1°C. The survival of the worms at the test temperature at regular time intervals is shown in Table II. The average survival time, or time at which 50 per cent of the individuals could be expected to survive is plotted against the number of days of conditioning at 22°C (Fig. 3). Very little if any conditioning effect is noted from the 1st to the 6th day, where the average survival time was between 10 and 15 hours. However, by the tenth day survival time is extended to 34 hours and on the 12th day 100% survival is noted in 48 hours, as is to be expected from the data on the upper lethal level of *P. hupeiensis* conditioned at 22° C. Worms living for this length of time were carried through to the following day. The only additional death was recorded for one animal on the 14th day, but as all others of this group survived it is probable that it had been injured previous to the experiment by improper handling. Thus *P. hupeiensis* requires about 12 days to adjust its lethal level to an increase in temperature from 15° to 22°C.

TABLE II. *Rate of thermal acclimatization to raised temperatures in* P. hupeiensis. *Experimental animals taken from 12°C were conditioned at 22°C from 1 to 18 days. Test temperature 24.1°C.*

Acclimatization time in days	Average survival time in hours	Per cent mortality in hours						
		1	3	6	10	23	29	48
1	13	0	0	0	33.3	100	..	....
2	15	0	0	0	16.6	100	....	. .
4	10	0	0	33.3	33.3	100	...	.
6	13	0	0	0	33.3	100	...	....
10	34	0	0	0	0	16.6	33.3	100
12	..	0	0	0	0	0	0	0
14	..	0	0	0	0	0	16.6	16.6
16	..	0	0	0	0	0	0	0
18	..	0	0	0	0	0	0	0

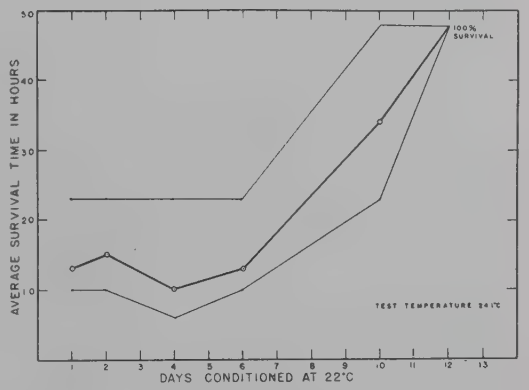


FIG. 3. Rate of thermal acclimatization to raised temperatures in *P. hupeiensis*.

This affirms the assumption made in the earlier experiments, that worms kept at an environmental temperature for a month could be expected to become fully acclimatized in that time.

CONCLUSIONS

The above experiments indicate that earthworms have rather low thermal tolerances. Both high and low temperatures cause a directive response, with worms tending to congregate in areas

where conditions are optimal for the species. Fraenkel and Gunn (1940) have pointed out the difficulties in the interpretation of temperature preferenda, as not only do the experimental conditions provide an environment different from the natural one in most cases, but variables other than temperature can also be operative in determining the results. Nevertheless, a general knowledge of an animal's temperature preferendum can be gained and comparisons between the reactions of different species under the same experimental conditions are extremely valuable. According to the terminology of Fraenkel and Gunn, thermotropism is not the proper term to be used in describing the reaction of moving organisms to temperature, as it is primarily a botanical term relating to curvature in plants and not to directive locomotory responses. Such a response, in which an animal moves toward or away from the source of stimulation but with regular bilateral deviations, is termed "klino-taxis." "Tropo-taxis" refers to directive responses in a straight path, without deviations. In observing the reactions of worms to the temperature gradient, the response seems to be a form of thermo-klino-taxis. As the animals were in uniform soil at saturation humidity it is probable that relative humidity, pH or chemical factors varied only slightly throughout the environment and initiated few if any directive responses.

The determinations on *P. hupeiensis* relative to conditioning temperature show the pronounced effects that the thermal history of an individual can have on its temperature tolerance. *P. hupeiensis* has thermal properties that are adequately suited to its natural environment. Temperature as a directive factor causes the worm to seek optimum environments where it can become acclimatized to the conservative temperature changes in the soil that follow seasonal changes in surface temperatures. It is unlikely in humid climates where the soil atmosphere is usually at or near saturation humidity that the wet-bulb reaction described by Hogben and Kirk (1944) for *L. terrestris* has any pronounced effect on worm populations. However, in agricultural areas where worms are frequently exposed to surface conditions this may be of considerable importance in allowing the animals to cool their bodies until they can burrow to cooler soil levels.

A. caliginosa had a wider temperature preferendum and a higher death point than either *P. hupeiensis* or *E. foetida*. Grant (1955b) has shown that this species is also more resistant to desiccation and has a higher vital limit of desiccation. These findings are in agreement with the fact that this worm has a wide habitat range and goes into a state of diapause within mucus-lined earth capsules when the soil moisture is reduced. The low moisture content of dry soils would tend to make them less stable thermally and therefore subject to considerable temperature fluctuations.

Summary

The low thermal tolerance of certain earthworms and the directive effect of temperature upon them has been demonstrated by a number of investigators. The present studies were concerned with temperature relationships in the megascolecid earthworm *Pheretima hupeiensis,* which occurs as a peregrine form in the eastern United States, and two common species of lumbricid worms, *Allolobophora caliginosa* and *Eisenia foetida.* The directive effect of temperature was studied on worms placed in a temperature gradient in a soil chamber. The temperature preferendum for *P. hupeiensis* was 15° to 23°C, for *E. foetida* 15.7° to 23.2°C and for *A. caliginosa* 10° to 23.2°C. The upper lethal temperature, defined as the temperature at which 50 per cent of the test animals could be expected to die in 48 hours, was 24.9°, 24.7° and 26.3°C for *P. hupeiensis, E. foetida* and *A. caliginosa* following acclimatization at 22°C. The effect of environmental temperatures on the upper lethal levels was studied in *P. hupeiensis.* Animals kept at 4°, 9° and 15°C had thermal death points of 19.4°, 20.9° and 22.7°C, there being an average gain in heat tolerance of 0.3°C for every 1°C rise in conditioning temperature. Individuals kept at 15°C took 12 days to acclimatize to a new environmental temperature of 22°C. These results indicate that *P. hupeiensis* is well adapted to humid soils where fluctuations in temperature are generally of a conservative nature. The directive and conditioning effects of temperature upon the worm allow it to seek soil levels of a non-lethal temperature and adjust itself to over-all seasonal changes in temperature. *A. caliginosa* has a greater thermal tolerance and is less sensitive to temperature changes.

References

Budington, R. A. 1902. Some physiological characteristics of annelid muscle. Amer. J. Physiol., **7**: 155-179.

Fraenkel, G. S. and D. L. Gunn. 1940. The orientation of animals. Oxford Univ. Press, 352 pp.

Fry, F. E. 1947. Effects of the environment on animal activity. Publ. Ont. Fish. Res. Lab., no. **55**: 5-62.

Grant, W. C. 1955a. An anatomical study of the peregrine megascolecid earthworm *Pheretima hupeiensis* in the eastern United States. Proc. Nat. Mus. In press.

———. 1955b. Studies on moisture relationships in earthworms. Ecology, **36**: 400-407.

Hogben, L. and R. L. Kirk. 1944. Studies on temperature regulation I. The Pulmonata and Oligochaeta. Proc. roy. Soc., **132B**: 239-252.

Hopp, H. and P. J. Linder. 1947. A principle for maintaining earthworms in farm soils. Science, **105**: 663.

McLeese, D. W. 1950. Factors limiting the survival of lobsters. Manuscript Rep. Biol. Sta., Fish. Res. Board Canada, No. **406**: 1-10.

Rogers, C. G. and E. M. Lewis. 1914. The relation of the body temperature of the earthworm to that of its environment. Biol. Bull. Woods Hole, **27**: 267-268.

———. 1916. The relation of the body temperature of certain cold-blooded animals to that of their environment. Biol. Bull. Woods Hole, **31**: 1-15.

Schmidt, P. 1918. Anabiosis of the earthworm. J. exp. Zool., **27**: 55-72.

Smith, A. C. 1902. The influence of temperature, odors, light and contact on the movements of the earthworm. Amer. J. Physiol., **6**: 459-486.

Wolf, A. V. 1938. Notes on the effect of heat in *Lumbricus terrestris* L. Ecology, **19**: 346-348.

NATURAL REVEGETATION OF SPOIL BANKS IN CENTRAL PENNSYLVANIA[1]

WILLIAM C. BRAMBLE AND ROGER H. ASHLEY
School of Forestry, Pennsylvania State University, University Park, Pennsylvania

Invasion of spoil banks by native vegetation is an important factor in reclamation of strip-mined coal land in Pennsylvania. An understanding of the development of natural plant communities and an evaluation of them must be regarded as an important part of planned reclamation, even though planting must be used for quick and satisfactory revegetation of nearly all areas.

The present paper covers the most common type of spoil found in central Pennsylvania. Spoil bank areas studied were unleveled, or only partly so, and were surrounded in part at least by woodlands. Important features of natural revegetation such as: the rate of the process, the pioneer plant community produced, the economic and aesthetic values of that community, and the amount of protective cover produced by it, were investigated.

METHOD OF STUDY

The 20 banks studied ranged from 2 to 35 years in age and were selected as representative of the most extensive spoil type in the region. This type is derived from acidic shale and sandstone, has a pH of from 4.0 to 5.5, and a fine soil content (less than 2 mm. diam.) of 20-50 per cent. In the younger ages, under 10 years, enough banks were taken to give a fair sampling of the normal range of conditions in the area. The older banks sampled, although few in number, represented a range from favorable to extremely unfavorable conditions typical of the region.

On the individual banks, sampling was done by using strip transects 6.6 feet wide, subdivided into milacre quadrats. At least 2 strips were taken per bank area, and were run at right angles to the general contour of the slopes. Visual estimation of per cent of ground surface covered was made on each quadrat. A count was made of stems of tree species occurring on the quadrats, while herbaceous vegetation and shrubs were tallied using a combined estimate of abundance and cover (A in Table II) and of sociability (S in Table II). This combined estimate (A) follows the system of Braun-Blanquet (1932) as given below:

+—sparsely, or very sparsely present; cover very small.
1—plentiful but of small cover value.
2—very numerous, or covering at least $\frac{1}{20}$ of the area.
3—any number of individuals covering $\frac{1}{4}$ to $\frac{1}{2}$ of the area.
4—any number of individuals covering $\frac{1}{2}$ to $\frac{3}{4}$ of the area.
5—covering more than $\frac{3}{4}$ of the area.

The estimate of sociability (S) was made on the following basis:

1—growing one in a place, singly.
2—grouped or tufted.
3—in troops, small patches, or cushions.
4—in small colonies, in extensive patches, or forming carpets.
5—in great crowds.

Thus, in the association table (Table II) in which the above system of classification is used, a + .1 indicates a species sparsely present and growing one in a place or singly, while the symbol 3.2 indicates a species covering $\frac{1}{4}$ to $\frac{1}{2}$ of the plot area and growing grouped or tufted. This system was found to be adequate for the information desired and represented a considerable saving in time over quadrats on which stems were counted. Symbols inclosed in brackets in Table

[1] Authorized for publication on July 6, 1954, as Paper No. 1884 in the Journal Series of The Pennsylvania Agricultural Experiment Station.

II indicate that the species was not found on plots, but did occur on the bank area.

In assembling data on the pioneer plant community in Table II, the term Constancy has been used as follows to express the per cent occurrence of species on milacre plots on the bank areas, studied:

Class I = on 1-20 per cent.
Class II = on 21-40 per cent.
Class III = on 41-60 per cent.
Class IV = on 61-80 per cent.
Class V = on 81-100 per cent.

Frequency in Table II has been used to show the distribution of species on a single spoil bank area, and is the per cent of the total quadrats on which a species occurred. Where average frequency is given, it represents an average of bank areas on which the species occurred.

Site Characteristics of Spoil Banks Important to Natural Revegetation

In the process of mining, topsoil is pushed aside with bulldozers and buried under overburden dug by power shovels as they uncover coal seams; the raw rock material from just above the coal is placed on top of the piles. These piles of mixed fine material and rock are left in long, parallel ridges, bare of vegetation and possessing many extremes of site conditions. The height of individual spoil piles and the size of any one spoil area depends primarily upon the depth to which an operation can go profitably, and the topography of the area. A common rule of thumb which gives a rough approximation of the depth of most operations is a 12 to 1 ratio, or 12 feet of overburden removed for each vertical foot of coal. Coal seams in Pennsylvania are commonly 3 to 6 feet in thickness and usually produced spoil banks from 15 to 30 feet high. As these seams usually dip into hillsides, only one to three cuts each about 60 feet wide are commonly made, which leave spoil areas about 100 to 300 feet wide and varying in length from a few hundred to thousands of feet. Only in a few cases where entire hilltops have been removed does any one operation affect more than 100 acres; ordinarily the spoil area created by a single operation does not exceed 20 acres.

Spoil banks thus created are sites which are generally unfavorable for plant invasion by seeds, and so are highly selective as to the dominant pioneer plants that appear upon them. Probably of most importance to plant establishment on raw spoil are those site factors which have a marked effect upon moisture in the environment, particularly on moisture in the surface layer of spoil.

Of marked importance in this connection is the fine soil content of the spoil, that is, particles less than 2 mm. in diameter. In the spoil type included in this study, the soil content in the upper 8 inches was very low in contrast to normal upland soils and lay between 20 and 50 per cent. Moreover, soon after banks have been exposed to weathering, a shale layer devoid of soil develops on the surface and acts as a barrier to invasion of the spoil by seeds. To successfully invade such spoil, seeds must either sift through the dry shale layer or be capable of rapid root penetration to moist soil beneath.

A second site factor of importance to natural invasion of spoil banks is wind exposure, which greatly affects plant survival through increased evaporation from spoil surfaces as well as loss from plants. As most spoil banks are exposed to the full sweep of wind from at least one direction, plants suffer from drought injury and from winter killing. Only the most hardy species survive as dominants in the pioneer community.

Two other factors which usually act together to have an important mechanical effect on plants are slope and looseness of spoil material. Unleveled banks have slopes which range from 30 per cent to 70 per cent, and, where the surface material is loose, a great deal of downslope movement occurs through frost and water action. This condition makes it so difficult for plants to become established that such unstable slopes may remain bare for 30 years or more.

Another important factor which causes death of young seedlings on spoil banks is high surface temperatures. Soil temperatures, particularly on dark colored spoil and southern exposures, have been recorded up to 130° F. on clear summer days in Pennsylvania. Even planted red pine seedlings, 2 years old, have been affected by direct heat injury. An example of those temperature extremes directly under the surface shale on leveled spoil, taken on August 7, 1951, in central Pennsylvania on dark, carbonaceous spoil, with a Taylor soil thermometer is given below:

Time of day	Air temperature (°F.)	Spoil surface temperature (°F.)
12:00 noon	77°	119°
1:00	74°	126°
2:00	81°	130°
3:00	79°	126°
4:00	79°	120°

Although soil acidity, which varied from pH 4.0 to 5.5 in the banks studied, was generally not un-

favorable to the species successfully invading the spoil, there were often extremely acid spots present with a pH of 3.5 or less on which no plants could become established. Occasionally, entire spoil areas were of this extremely acid nature and remained barren after 15 or 20 years or more. This peculiar acidic condition is commonly caused by the presence of pyritic material in the shale overburden or in roof coal, which breaks down upon exposure to air to form sulfuric acid. Soluble alumina, also, is formed by reaction of the acid on pyritic shales and is harmful to many plants.

Invasion of Spoil Banks by Vegetation

Other things being favorable, it was expected that the pioneer species dominant on spoil areas would be those plants which are found growing on the edges of land bordering them. However, the severe site conditions of the raw spoil, previously described, act to permit only a few of the possible species to become established.

Examination of the list of characteristic and common pioneer species (Table II) reveals that invasion of successful species may occur from considerable distances through seed adapted to wind or animal transportation. Aspen invades by means of windborne seeds, often from stands quite distant from the banks. Evidently the aspen seed sifts through the crevices in the shale surface and encounters a suitable medium for germination. Red maple is another species of the pioneer community with seeds adapted to wind dissemination, although for shorter distances. Other dominant pioneer species, namely fire cherry, sumac, sweetfern, and blackberry are brought in by birds and small mammals which use the spoil banks. Although scattered plants may appear from parts such as roots and rhizomes which were mixed with the spoil in mining, these are of minor importance in the total cover. Invasion of topsoil areas is also of minor importance except on certain edges.

Rate of Development of a Vegetation Cover

During the first 3 years after raw spoil has been deposited in mining, it is nearly barren of vegetation. A change in plant cover becomes apparent at about the fourth year (Table I), and from then on the rate of development varies greatly depending upon the favorableness of the site factors existent on any particular area. However, the total cover does not appear in any case to exceed 50 per cent during the first 10 years (Fig. 1), and on banks with loose shale slopes, it may remain as low as 15.1 per cent for at least 29 years.

Table I. *Rate of development of vegetation cover on spoil banks*

Bank number	Age (years)	Per cent of ground surface covered with vegetation
1	2	0.1
2	2-3	0.1
3	3	2.5
4	3-4	15.4
5	3-4	13.9
6	3-4	4.7
7	4	3.8
8	4-5	7.0
9	5	8.4
10	5	12.9
11	6	27.9
12	6	18.7
13	6-7	21.9
14	8	15.1
15	9	45.4
16	9	30.8
17	10	33.4
18	25	29.0
19	29	15.1

As is typical of adverse sites in general, the most favorable spots on spoil banks are occupied fairly rapidly and then the area remains more or less in a static condition in so far as additional cover is concerned. In fact, the cover value at 4 to 5 years may be as high as it will get for the next 20 years on many banks. Most increases in cover during this period are due to increase in size of plants or centrifugal spread of plants established in favorable spots, not to new spot invasions of bare areas. The unoccupied, more adverse, spoil areas remain bare for many years. For example, a spoil bank laid down in Centre County, Pennsylvania, during World War I, comparable in height and size to those now being created (Fig. 1), has been found to possess a sparse tree layer, a spotty shrub layer, and a very scant ground layer.

The probable reason for the lack of vegetative development on certain parts of spoil areas, even though of similar pH and soil content as other areas which have been successfully invaded, appears to lie in a development of surface adversity. As banks age, they develop a loose shale layer on their surfaces which inhibits invasion owing to rapid drying and downslope movement. That the cause lies in these surface conditions rather than total unfitness of the spoil for supporting plant life has been borne out by the successful planting of slopes of a bank that had remained bare for 29 years.

The Pioneer Community

The first definite plant community developed on unleveled spoil banks in central Pennsylvania is a tree-shrub mixture, accompanied by a char-

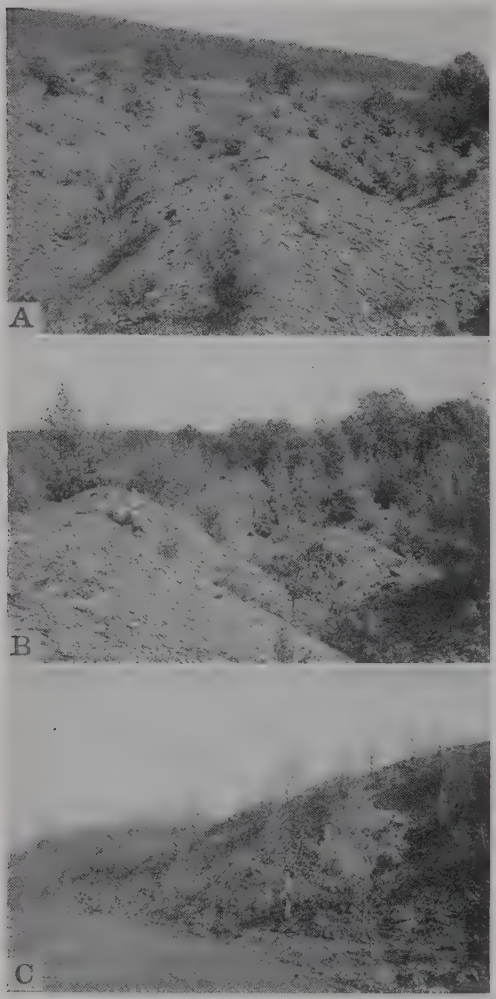


FIG. 1. Development of the aspen-fire cherry association in central Pennsylvania. A. On a 6 to 7 year old spoil bank; total cover is 21.9 per cent. B. On a 10 year old spoil bank; total cover is 33.4 per cent. C. On a 35 year old spoil bank; cover is about 50 per cent.

acteristic group of sparse herbs and grasses. There has not been a definite lichen or herb-grass stage preceding the tree-shrub community such as has been described for plant succession on spoil areas in the mid-west by Croxton (1928) and McDougal (1918), probably owing to differences in spoil type and topographic location. This development of a pioneer tree-shrub community on spoil banks is unusual, but is not unexpected on exposed sites with a soil surface composed primarily of loose shale containing a very low proportion of fine soil material. Both Weaver and Clements (1938) and Braun-Blanquet (1932) have described similar pioneer communities on comparable substrata such as rock slides and talus slopes.

The pioneer community developing on spoil banks in central Pennsylvania has been designated as an aspen-fire cherry association from the dominant and characteristic species of trees and shrubs constantly present. Use of the term "association" essentially follows the concepts of Braun-Blanquet (1932). This association is apparently related to the aspen-fire cherry forest cover type of the region, which appears on a wide range of sites on severely burned areas as an initial stage in secondary succession. Studies of this forest cover type in the course of this study has shown its marked similarity in species composition where it occurred on comparable sites.

An association table has been drawn up (Table II) to show the floristic composition of 19 banks examined. In this table, the banks over 5 years old have been separated from younger banks in order to emphasize the consistent composition of the association for at least 29 years. Aspen (*Populus grandidentata* and *P. tremuloides*) and fire cherry (*Prunus pensylvanica*) dominate the tree layer of this community while red maple (*Acer rubrum*) appears as a characteristic species of lesser abundance. Blackberry (*Rubus alleghenicnsis*) is the most prominent shrub with sweet fern (*Comptonia peregrina*), sumac (*Rhus typhina* and *R. glabra*), and prairie willow (*Salix humilis*) as additional characteristic species. Ten herbs and grasses, common to upland abandoned fields of the surrounding territory, appear as sparse but constant components of the association. The herb layer is of low cover value on the unleveled banks included in this study; however, on leveled banks of high soil content, a typical old-field community dominated by poverty grass (*Danthonia spicata*) and dewberry (*Rubus flagellaris*) often develops prior to the tree-shrub community described above. This old-field community also appears on top-soil areas on the edges of banks and on spots within spoil areas where top-soil had been deposited in the mining operation.

VALUE OF THE PIONEER COMMUNITY

The value of the aspen-fire cherry association in reclamation of spoil banks must be considered from several points of view. Any vegetation becoming established on spoil areas, whether planted or established by natural invasion, should have value either as a producer of economically valuable wood

TABLE II. *Association table for the pioneer* aspen-fire cherry *association on spoil banks in central Pennsylvania. A = abundance and cover estimate, S = sociability, C = constancy, F = frequency, as explained under "Method of Study." Scientific names are from Fernald (1950)*

Number of banks	10		9		Average of all banks
Age of banks (years)	2–5		6+		
Average total plant cover	6.9		26.4		16.1
Common and characteristic species	A.S	C/F	A.S	C/F	C/F
Tree layer					
Acer rubrum	+.1	V/12	+.1	V/10	V/11
Populus grandidentata	+.1	V/17	±2.1	IV/20	V/19
Populus tremuloides	±2.1	V/24	±2.1	V/17	V/20
Prunus pensylvanica	+.1	V/8	±2.1	V/21	V/15
Shrub layer					
Comptonia peregrina	(+.1)	I/0	+.3	IV/5	III/3
Rubus allegheniensis	+.2	V/16	±2.2	V/46	V/33
Rhus typhina	+.1	II/2	+.1	IV/8	III/5
Rhus glabra	....	....	+.1	III/4	II/2
Salix humilis	+.1	II/1	+.2	IV/5	III/3
Herb layer					
Aster spp.	±1.1	V/14	+.1	V/12	V/13
Carex spp.	±1.2	IV/18	+.2	IV/5	IV/11
Danthonia spicata	±1.2	IV/18	+.2	V/18	IV/18
Hieracium spp.	+.2	IV/6	+.2	III/3	IV/4
Lysimachia quadrifolia	+.1	IV/4	+.1	IV/4	IV/4
Panicum spp.	±1.2	V/20	±1.2	V/14	V/18
Poa compressa	+.1	III/7	+.1	IV/3	IV/5
Potentilla canadensis	+.2	III/9	+.2	IV/5	IV/7
Soliago spp.	+.1	V/28	+.2	V/14	V/20
Viola fimbriatula	+.2	IV/13	+.2	IV/7	IV/10
Companion species*					
Tree layer					
Robinia pseudo-acacia	+.1	III/2	+.1	II/2	III/2
Amelanchier arborea	+.1	I/1	+.1	II/1	II/1
Betula nigra	+.1	III/2	+.1	II/1	II/2
Quercus rubra	(+.1)	I/0	+.1	III/2	II/1
Sassafras albidum	(+.1)	I/1	+.1	II/1	II/1
Shrub layer					
Aralia spinosa	+.1	II/1	+.1	II/2	II/1
Cornus racemosa	....	....	+.1	I/1	I/1
Diervilla lonicera	+.2	II/3	+.2	II/8	II/6
Gaultheria procumbens	(+.1)	I/0	+.2	II/1	II/1
Hamamelis virginiana	(+.1)	I/0	+.1	II/2	II/1
Rubus occidentalis	+.1	I/2	+.1	II/1	II/1
Rubus flagellaris	....	....	+.1	I/1	I/1
Sambucus canadensis	+.1	I/1	+.2	II/1	II/1
Sambucus pubens	(+.1)	I/0	+.2	II/2	II/1
Vaccinium angustifolium	(+.1)	I/0	+.2	II/2	II/1
Viburnum acerifolium	(+.1)	I/0	+.1	II/1	II/1
Vitis spp.	+.1	I/1	+.1	III/1	II/1
Herb layer					
Agrostis spp.	+.2	V/7	+.2	II/1	III/3
Apocynum cannabinum	+.1	I/1	+.1	IV/1	III/1
Erechtites hieracifolia	±1.1	V/11	+.1	II/1	III/5
Pteridium aquilinum	+.1	II/1	+.3	III/6	III/3
Rumex acetosella	+.2	III/3	+.2	II/3	III/3
Acalypha virginica	+.1	II/1	....	....	II/1
Achillea millefolium	+.1	II/1	+.2	II/2	II/1
Ambrosia spp.	+.1	III/1	+.1	II/1	II/1
Chrysanthemum leucanthemum	+.2	II/9	....	....	II/4
Cirsium vulgare	+.1	II/1	+.1	I/1	II/1
Convolvulus spithamaeus	+.1	I/1	+.1	III/7	II/4
Daucus carota	+.1	II/4	+.1	II/1	II/2
Dennstaedtia punctilobula	+.1	II/1	+.1	II/1	II/1
Fragaria virginiana	+.2	I/1	+.2	II/1	II/1
Hedeoma pulegioides	+.1	II/2	+.1	I/1	II/1
Lactuca canadensis	(+.1)	I/0	+.1	II/1	II/1
Lepidium virginicum	+.1	II/1	+.1	I/1	II/1
Lobelia inflata	+.1	II/1	+.1	III/1	II/1
Oenothera biennis	+.1	III/1	+.1	I/1	II/1
Oxalis spp.	+.1	I/1	+.1	II/1	II/1
Potentilla norvegica	+.1	II/1	+.1	II/1	II/1
Polygonum scandens	+.1	II/5	+.2	II/5	II/5
Polygonum spp.	+.1	III/1	(+.1)	II/0	II/1
Prenanthes trifoliolata	+.1	II/1	(+.1)	I/0	II/1
Taraxacum officinale	+.1	III/1	+.1	I/1	II/1
Veronica officinalis	+.3	II/3	+.3	II/1	II/1
Viola spp.	(+.1)	I/0	+.1	III/5	II/2

*51 species of herbs and grasses, 12 species of shrubs, and 13 species of trees have been omitted from this table as casual invaders of little importance.

products, a wildlife habitat, an aesthetically desirable cover, or some combination of these.

With respect to production of wood products, the natural stocking of spoil banks with trees on the whole has been found to be very poor, with few exceptions. In Table III, in which one seedling per milacre quadrat was needed to classify a quadrat as stocked, only 2 banks were more than 60 per cent stocked, 7 were between 40 and 60 per cent stocked, and 8 were less than 40 per cent stocked. The average stocking for all banks studied were 36.2 per cent. When this is compared to a standard of 60 per cent, often taken as successful planting survival, it may be seen that natural reforestation on the whole has not been adequate. Moreover, none of the banks were more than 15 per cent stocked with tree species other than low value aspen, fire cherry, and red maple.

It is obvious that the potential value of the ty as producers of wood products must be rated common species appearing in the pioneer communivery low. Aspen is normally considered a satis-

TABLE III. *Stocking of spoil bank areas with trees*

Bank number	Age (years)	No. quadrats taken	No. trees per acre	Per cent milacre quadrats with 1 or more trees
3	3	23	400	8
4	3-4	31	8830	93
5	3-4	35	1970	45
6	3-4	34	1590	64
7	4	73	10	1
8	4-5	41	1630	54
9	5	54	60	2
10	5	89	430	26
11	6	55	1040	44
12	6	51	960	42
13	6-7	55	1290	45
14	8	57	190	14
15	9	23	1050	48
16	9	34	560	35
17	10	129	1300	55
18	25	78	190	19
19	29	112	370	21

factory pulpwood species in the area under study only on best sites. On poor sites, particularly where trembling aspen is dominant, the species seldom reaches a size where profitable pulpwood cutting is possible before the stands deteriorate. This deterioration occurs at 20 to 30 years, when the trees are about 4 inches in diameter at breast height. On spoil banks at 29 to 35 years of age, aspen is of extremely poor form and is practically worthless as a pulpwood crop.

The common fire cherry is not of commercial value for wood products of any kind, while red maple and black cherry, species which could produce wood products of value, occur but sparsely and are of poor form. Other native species found on spoil banks, such as red oak, white ash, white pine, yellow birch, and sugar maple, which offer promise of timber production, are of such infrequent occurrence that their present value is very low. Undoubtedly the banks will eventually develop into a productive forest unit as the pioneer aspen-fire cherry is superseded by some other forest community. The exact type of forest that will succeed the pioneer community will vary with the location of any particular spoil area. In most cases, however, it will be an oak-hickory mixture somewhat similar to that described recently on century-old ore banks in West Virginia by Tryon and Markus (1953).

The game cover value of natural vegetation coming in on spoil banks is also very low. The average cover value for all vegetation on 19 banks included in this study during the growing season amounted to 16.1 per cent, and ranged from 0.1 to 45.4 per cent. The highest cover value was found on banks invaded by black locust, which spreads by root suckers. Unfortunately, such banks were the exception rather than the rule. While no special study of wildlife usage was made, only rarely were birds or small mammals observed using vegetative cover on spoil banks. The attraction of the banks for such animal life as used by them seemed to lie more in their open, rocky nature and in the possibility of obtaining shelter among the crevices that are often present. It is possible that birds using the banks are attracted to them by their open condition and as a source of grit and dusting places. Since practically all the tree species on the banks were deciduous, the winter cover value was exceptionally low.

Some game food is produced by the common trees and shrubs occurring naturally on spoil banks. Fire cherry and blackberry both produce fruit used as food, while sparse browse for deer and rabbits is furnished by the woody vegetation. Deer use spoil bank areas as travel lanes and watering places, and have been observed to browse heavily on fire cherry during the early fall season. Some evidence of the pressure for food on spoil banks was obtained when artificial seeding was attempted on the banks. Seeds sown in the fall and winter were soon taken by small rodents and birds. In fact, successful seeding of oaks was established only by planting in late March, about the time when the acorns were germinating. Evidently the seeds germinated and the seedlings became established before they were discovered and utilized by rodents. Trapping experiments showed that deer mice (*Peromyscus* sp.) were particularly abundant.

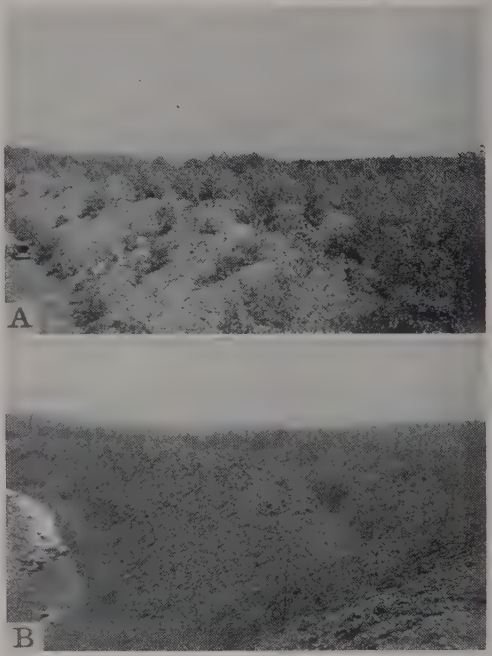


FIG. 2. Aspen-fire cherry association which has produced 33 per cent plant cover on a 10-year spoil bank area in central Pennsylvania. The banks are 55 per cent stocked with trees which average 1300 stems per acre. A. Summer aspect; B. Winter aspect.

Although natural revegetation of unleveled spoil banks tends to slowly improve their appearance, the aesthetic value of such vegetation during the first ten years is very low, particularly when compared to the cover that can be obtained from artificial planting. A lack of evergreens in the natural vegetation results in a particularly barren aspect in the winter months.

SUMMARY

An investigation of the development of natural vegetation was made on 20 spoil banks in central

Pennsylvania ranging from 2 to 35 years in age. Owing to severe site conditions, the pioneer community was dominated by trees and shrubs capable of invading highly unfavorable sites by means of seeds transported by wind and animals, often from considerable distances. An aspen-fire cherry association has been described as the most common dominant pioneer plant community found on upland spoil banks. Aspen, fire cherry, and red maple were the common and characteristic species of the tree layer. Blackberry, sweetfern, sumac, and prairie willow were characteristic shrubs. A sparse layer of herbs and grasses formed the ground layer. The stocking with trees averaged 36.2 per cent and was of low value for production of wood products. Game cover and food produced was of low value, also; but surprisingly frequent use was made of spoil areas by certain animals, particularly deer mice. Aesthetically, natural plant cover offers but a sparse and unattractive cover for spoil areas for at least 35 years.

References

Braun-Blanquet, J. 1932. Plant sociology. (Transl. by G. D. Fuller and H. S. Conard) McGraw-Hill Book Co., N. Y. 439 p.

Croxton, W. C. 1928. Revegetation of Illinois coal-stripped land. Ecology 9: 155-175.

Fernald, M. L. 1950. Gray's manual of botany. 8th ed. American Book Co., N. Y. 1632 p.

McDougal, W. B. 1918. Plant succession on an artificial bare area in Illinois. Trans. Ill. Acad. Sci. 11: 129-131.

Tryon, E. H., and Rudolfs Markus. 1953. Development of vegetation on century-old iron-ore spoil banks. West Virginia Agr. Exp. Sta. Bull. 360. 63 p.

Weaver, J. E., and F. E. Clements. 1938. Plant ecology. McGraw-Hill Book Co., N. Y. 601 p.

POPULATION CHANGES AND ROOSTING TIME OF STARLINGS

David E. Davis

The Johns Hopkins School of Hygiene and Public Health, Baltimore, Maryland

The factors governing the time of roosting and awakening of birds have received considerable attention for a number of years. The starling is suitable species for study of this problem because birds roost nightly in a particular spot. Presumably the same individuals return although proof of this point is lacking (Rowan 1938). This paper describes the roosting time of a flock at Baltimore from December 1950 through 1952. Attempts to analyze the factors controlling roosting time will be mentioned.

In connection with the observations of roosting times, counts were made of the numbers of birds almost every week from December 1950 till May 1954 (the counts are being continued). From these counts the changes in numbers of roosting birds can be discerned.

The birds roosted in two towers on a building of the Johns Hopkins Hospital (Fig. 1) as well as in the vines on the buildings. The roost was definitely used in 1948 and 1949 and probably before that time although no observations were made. In the evening the birds approach the roost from the northeast, swerving around and over a tall building just northeast of the roost The towers have louvers through which the birds entered. Many birds roosted on the louvers and others roosted on a platform in the upper part of the tower. A trap was made in February 1952 to catch birds on the platform but no attempt was ever made to catch birds on the louvers for fear of scaring them away. Both towers had an updraft of warm air from the building.

The counts of the starlings were made from the roof of a building directly north of the towers. Since almost all birds came from the northeast it was easy to set up boundaries to the observation area and exclude a trivial number that came in from directly north and for practical reasons could not be counted. The observer arrived on the roof 5-10 minutes before the birds began to arrive and then counted and recorded the number of birds that arrived during 5-minute intervals. The early and late counts were accurate to individuals since small numbers came in at a time but as larger numbers arrived, the birds were usually counted by tens. At the time of peak arrival, when several hundred entered in 5 minutes, the birds were counted by fifties or even hundreds. The errors in the counts are probably small because of the practice of counting small numbers at the beginning of each day. Since the true number of birds is not known the extent of the error cannot be known. However, since all

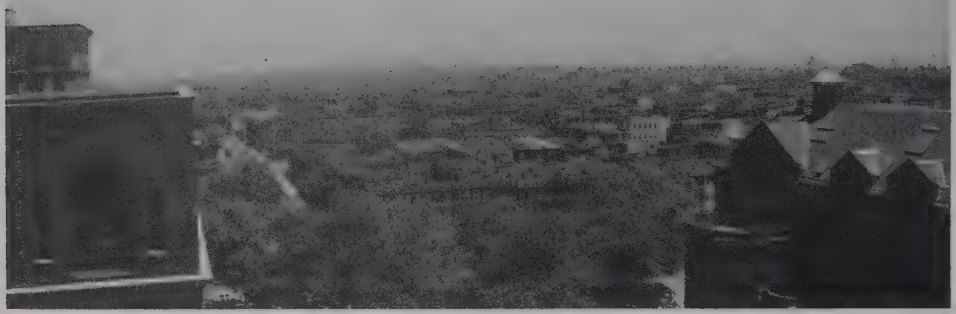


FIG. 1. Observer's view of the area of flight to the roost. The birds came around the tall building on the left and roosted in the tower and on the vines of the buildings on the right.

observations were made by 2 persons who agreed closely and since all data are in relative terms the error in counts does not alter the conclusions.

A total of 281 counts was made from December 19, 1950 to May 14, 1955. Till February, 1952 about 3 counts per week were made; after that date about one count per week was done. The days for the counts were chosen randomly in the sense that the choice depended upon schedules for other work rather than upon the weather or factors that concerned the starlings.

In addition to the number of birds, a record was made of the reading on a Weston Photometer pointed at the zenith, the relative amount and direction of wind, and degree of cloud cover. Temperatures were recorded till the relation to weather bureau data was established and then those records were used. It is useless to compare the numerical photometer values here obtained with those of Nice (1935) because of differences in meters and technique.

The problem of an end point for the roosting time of starlings presented difficulties. The time that the first or last bird arrived obviously would be greatly affected by chance. Preliminary tests with several end points suggested that the time by which 50% of the birds had arrived was the end-point least influenced by chance variation. This point was determined to the nearest minute. All times were Eastern Standard. Civil sunset time was obtained from the Baltimore branch hydrographic office of the U. S. Navy.

The literature on starlings is extensive but only some of it is pertinent to the problems considered here. The references will be summarized under several headings. Population changes during the year have been recorded in a few cases. Hickey (1943: 61) gives data for 18 counts during a year of the number of birds arriving at a building in New York City. The major peak was in late November and the minor peak was in late March. Nichols (1939) recorded the number of birds seen from a train and found the lowest numbers in April-May and the highest in July-August. Rowan (1938: 67) reports that the numbers at a roost in London varied each night (no counts) and that the total declined till January 23 then increased to a peak on February 17 and then declined in April. Population changes from year to year were noted by MacPherson (1928: 226) and Mayr (1947: 37).

Descriptions of winter roosts have been made by many authors, especially European, and will be considered only briefly here since a description of the roost is not the primary object of this paper. Woodruffe-Peacock (1918: 112) describes clouds of starlings that roosted in a thicket till the bushes were cut down. Roebuck (1934) lists 118 roosts in England that contained 400,000 birds and estimates 3 million birds or one per acre for the region. Not all birds roost in large aggregations for Koch (1930) reports a few birds roosting in eaves away from a large roost. Boyd (1932) describes a roost in a fox covert, where the birds increased during a cold spell in January and remained till March or April. Wynne-Edwards (1929) observed that the birds collect in trees before roosting. A roost had been in a reed-bed for 132 years. Cruickshank (1937) described a roost in a Phragmites marsh on Long Island, N. Y. About 150,000 starlings and many thousand grackles spent the night in an area that had been used for at least 5 years. The birds required only one hour to arrive but came from 20-30 miles in a series of hops. Low (1924) describes the gathering of starlings in several areas before actually going to the roost. Marples (1934) indicates that starlings have increased during the past 100 years. One roost has been in use for 180 years and 107 out of 247 roosts had been in use for more than 10 years. About 15-20 thousand birds roosted in London. Some evidence is cited that suggests that warmth is a factor in the choice of site.

Starlings began to roost in London about 1900 (Fitter 1949: 46; Rowan 1938). A peculiar location is reported by Kennedy (1928) who found starlings roosting on the ground and forming tunnels in the thick grass. The direction of flight to the roost has been noted by Hickey (1943: 61); Marples (1932: 314); Forrest (1900: 131); Cummings (1908: 121); Brown (1946) and Thomason (1932). These authors indicate that the flight lines are direct and generally fixed but that several lines may cross or diverge in a particular area. Hale (1934) traced birds from the center of London to a farm about 8 miles away. Bullough (1942) made extensive observations on the contrast in roosting behavior of Continental and British races of starlings. The local birds left the roosts in January but the Continental birds remained till March, when they migrated. He states (without data) that many males roost communally while the female broods the young and that, about 12 days after the young hatch, both adults may go to communal roosts. Morley (1939) describes a pair that roosted away from their nest hole from November to January but then began to roost nearby. He (1941) also describes the territorial behavior of birds during the winter and the fact that local birds may roost near the territory rather than with the large flocks.

Summer roosts have also been described frequently. Tischler (1908) reports males and females roosting in the breeding season and Elliot (1930) describes 2,000 birds in a thicket in summer while Williamson (1947) reports the roost of a non-breeding flock. Boyd (1932) states that some birds roosted in the covert all year and Kluijver (1933) describes the roosting of birds in boxes. Several authors have collected birds at summer roosts. Withersby (1929) found that 7 out of 26 males collected from April 19-May 23 were not breeding but that some females had an incubation patch. Tischler (1905) obtained 17 birds from May 24-June 1; all were males but only 8 had fully developed testes. Savage (1922) got 9 birds on June 1 of which 3 males were in breeding condition but 4 males and 2 females were not.

The factors controlling roosting or rising have been studied in several species. Schwan (1921-22) summarized a number of annecdotes about song and weather factors. Odum (1942: 518) reported roosting times for chickadees and Urner (Hickey, 1943: 58) for herons. Brackbill (1952) noted that several species of ducks left a reservoir each at a rather consistent time in relation to sunset. Although the factors controlling roosting time of tits are not discussed in detail Hinde (1952: 168) summarizes the results of observations by various authors in 5 localities in Europe. Roosting times in Holland and England were similar but in Munich the times were somewhat later. There is a marked seasonal change in roosting time in relation to sunset especially in the north (Lapland).

Kluijver (1950) gives a detailed description of the roosting times of a male and of a female great tit and determines the correlation coefficients for cloudiness, wind speed and temperature. Weather conditions have little influence on the time of roosting although the coefficients for cloudiness were about —0.3 An interesting experiment, however, suggested that the food supply might be influential. Radford (1954) from a study of the roosting and awakening of the European nuthatch expressed some opinions about the factors controlling roosting. The birds roosted early on some but not all dark days. On some cold days they roosted late. His extensive data showed that the birds roosted essentially at sunset from October 12 to March 22.

Seibert (1951) recorded light intensity at roosting times for 4 kinds of herons. Each species arrived at a regular time in relation to sunset and left in the morning at a lower light intensity than that at the roosting time. Variations in light intensity had no obvious effect. Brauner (1952) concluded from 38 light readings that poor-wills began evening activity earlier on dark days than on bright days but the data are not presented in detail. Dunnett and Hinde (1953) observed that 4 captive great tits roosted at sunset in October but by February were roosting about 30-40 minutes before sunset. Variability was very great, however, and the tendency claimed by the authors for earlier roosting on cloudy days is not supported by their data. Miller (1954) noted that the regular roosting schedule of a sparrow hawk was not altered by overcast skies. Haartman (1952) and Scheer (1952) attempted to find whether temperature affected the time of morning song but the results were inconclusive.

Seasonal changes have been noted regularly. Haartman (1948) noted for swifts (62 observations from May 22-September 8) that the time between sundown and sleep was the greatest at the summer solstice and that the birds went to rest earlier on cloudy days. Hinde (1952) found that wild great and also blue tits roosted at sunset in October and about 15 minutes before in March. Hinde (1952: 176) also observed 2 great spotted woodpeckers and found that they roosted at sunset in November but more than half an hour before sunset in February and March. A nuthatch showed the same change. Nice (1943) in a comprehensive discussion of song at morning and evening reports that there was little seasonal difference in the time of settling down at night. The time, however, appeared to differ on cloudy and clear days. It was about 13-14 minutes after sunset in clear weather and about 3 minutes in cloudy. Hansen (1952) observed the calling time of owls (*Strix aluco*) for 2 years and found that the calling stopped earlier and started later in relation to sunrise and sunset in winter than in summer. Kendeigh (1952: 77) gives a graph for the house wren showing activity in relation to sunset during the nesting season when incubation influences the times. Hinde (1952: 171) found for 3 females that the bird went to roost much earlier during incubation than during laying. Pynnönen (1939) reported that individual woodpeckers (Dryobates) went to sleep (roost) shortly before sunset in winter but about 3 hours before in summer.

A number of articles discuss roosting times at high latitudes. Armstrong (1954) reviewed the behavior of birds in continuous light and found little positive evidence about any particular causal relation. Cullen (1954) examined the roosting of seabirds but made no measurements of light intensity. Karplus (1952) measured the light intensity and found that several species roosted at the lowest values. Franz (1943) describes some miscellaneous observations on 8 species and found that the birds roosted later in relation to light in December than in October and March. Palmgren (1949) states that light is not the only factor (because they wake at usual time in constant darkness), but is important, although he presents no measurements.

For starlings a number of observations of roosting times have been made. Campbell (1902) and Secker (1954) recorded some miscellaneous times of flocking. Boyd (1932) reports that the birds roosted an hour before

sunset. Nice (1935) gave some photometer readings and noted that the rising and roosting times of a resident pair were related in general to sunset. Reif (1944) gave some arrival and departure times at Wilkes-Barre, Pa. The birds began to leave the roost shortly after dawn but some did not leave till 11 a.m. The birds returned between 1645 and 1656 EST on January 12. Wynne-Edwards (1929) abandoned the study of light intensity in relation to time of leaving the roost because of the uncertainty of the measurements. He concluded that intensity of light is not important but suggests that rate of change of intensity might be. His data are the time in relation to sunrise that flocks passed overhead. He (1931) also suggests, based on circumstancial evidence, that birds with the most mature gonads leave the roost earliest and return the latest each day. Brown (1946: 77) published a table showing the time of assembly for 14 afternoons from November 4 to March 10. During November the assembly was half complete by sunset; during January it was practically complete; during February and March it was less than half complete. Six departure times were recorded.

Results

The changes in number of roosting birds during the year will be discussed first because of their value in understanding the roosting data. Figure 2 shows the total number of birds flying into the roost (towers and vines) for each week. The weekly data for the first 13 months are averaged from about 3 observations per week; the subsequent data are based on about one observation. The detailed daily data are omitted as well as statistical parameters since tests of significance of differences are unnecessary in this discussion of changes.

The increase in numbers in winter and the decline in summer are obvious. It is important to note that a few birds came into the roost every evening; the lowest number was 2 birds on an evening in the 23rd week (June) of 1952.

Another obvious change is the increase in early fall (September), a decline in the early winter, and then an increase again in January and February. In December 1950 the observations began apparently at the time of the late winter increase. The early beginning (December) of this increase is rather puzzling. It seems too early to agree with spring migration but it does coincide with the time that local birds begin to use nest boxes. The total number of birds was clearly greatest in the winter of 1951-52 and least in 1952-53. An explanation for the small number in the latter winter is not readily apparent. In February 1952 a program of collection of birds was begun. About 100 birds were killed and examined for sex, age, and reproductive condition each week (results to be reported elsewhere). At first the trap caught about 300 birds and the number over 100 was liberated. About 700 birds were killed during February and March when the collections were stopped for lack for birds. At that time the decline was attributed to the removal in spite of the lack of proof that the same birds use the roost each nght. In 1952-53 the birds began in September to use the roost as usual but suddenly the numbers dropped even though no trapping was done. Examination of the roost itself revealed no cause for decline. The low numbers continued during 1953 when a few hundred birds

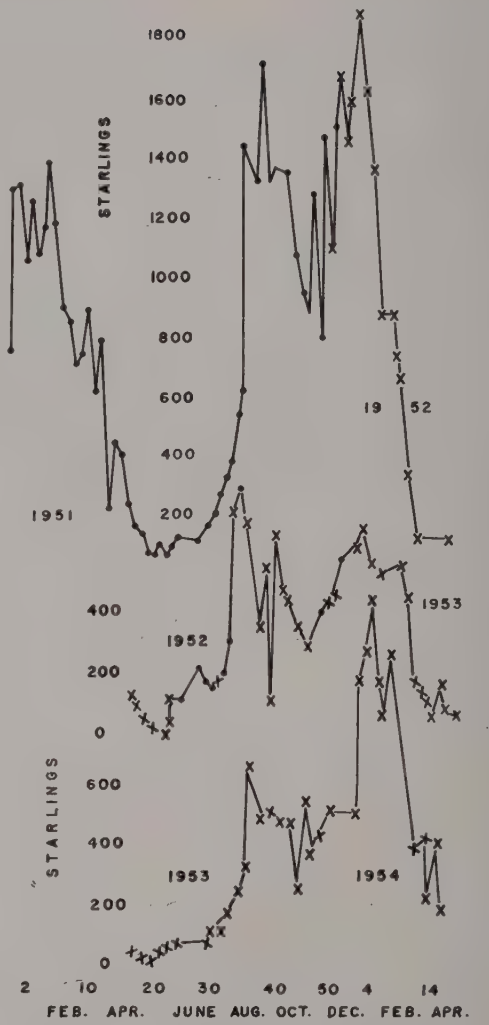


Fig. 2. The number of birds flying into roost by weeks from 1951 to 1954. The counts for each year are placed above one another to show the constancy of the week of changes in roosting population numbers. (Crosses mean one observation per week. Dots mean 2-4 observations per week).

were banded. The similarity of the shape of the curves for the two winters suggests that some general effect caused the difference in magnitude. A possibility is that the mild winter of 1952-53 permitted the birds to roost elsewhere.

The changes for the three and a half years show a striking uniformity in date of occurrence of the population changes. Table I shows the week of occurrence of 6 events in the cycle and also the approximate part of the month for the event.

TABLE I. *The week of changes in numbers of starlings*

Year	Week Event Occurred				Month
	1951	1952	1953	1954	
Early Spring Maximum..	6	5	4	5	late Jan.
Spring Decline.....	13	11	10	9-10	early March
Minimum Number.....	24	23	19-23	23	early June
Early Fall Increase.....	37	34	36	34	late August
Early Fall Maximum....	41	36	37	42	Sept.-Oct.
Early Winter Low.....	50	47	45	46	November

Considering the fact that only one count per week was made in most years and the somewhat arbitrary assignment of dates, the agreement in timing is very close. One gets the impression that photoperiod rather than weather is the governing force.

The time of roosting can be presented most vividly when plotted as the difference between the time of sunset and the time at which 50% of the birds arrived (Fig. 3). It is at once apparent that the birds arrived half an hour before sunset in the winter, almost at sunset in the spring, and almost an hour before sunset in late summer. The constancy of the relation to sunset from November to March is in contrast to the change reported by Brown (1946), and also to the change in relation to sunrise (Wynne-Edwards 1929) from 9 minutes before in December to 6 minutes after in February. A general correlation of the changes with the breeding season is at once obvious but the detailed history of individuals is not known. It is possible that the birds that roost in April are unsuccessful contenders for a nesting site or really functionally not breeding. The early arrival in August cannot be a function of the length of day because the days in April have the same length. Several other possible explanations can be suggested but discussion of this problem must await detailed knowledge of the individuals involved.

The extent of variability of arrival time is not presented in detail because no use is made of it in this paper. However its extent can be seen from the dots and crosses in Figure 3 which are the individual observations. (The dots are the average of 2-4 evenings per week.) A sample is

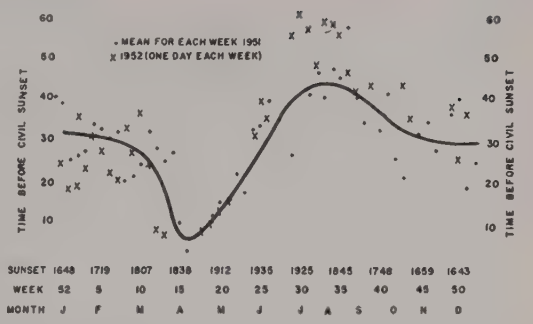


FIG. 3. The relation of season to time before sunset by which half the birds had arrived. The time of sunset is the horizontal base line. The dots represent the mean of 2-4 counts per week in 1951. The crosses refer to 1 count per week in 1952. The smoothed line perhaps should be drawn higher for August.

presented in Table II. In an attempt to understand the factors controlling roosting time an extensive statistical analysis was made of the correlation of the 50% point and the photometer readings, temperature, wind, and cloud cover. In brief, no correlation of any of the measurements was detected. For example the table shows a rather constant photometer reading (60-75) for the time at which 50% of the birds arrived but on November 13 the reading was double (125). Such discrepancies were adequate to prevent a demonstration of a correlation.

The photometer reading (50% arrival) differed greatly for the various periods. From October to March it averaged 71.8 ($N = 68$; S.D. = 24.1); from March to July it averaged 46.5 ($N = 40$; S.D. = 20.1). The difference is significant. For July to October it averaged 121.0 ($N = 20$) but the variability was very great. Clearly the birds roost at different light intensities at different seasons but their daily roosting time is very variable in reference to light as measured by a photometer. These results mean either that there is no correlation between these factors and roosting time or that the measurements were not suitable. No correlation with rate of change of light intensity as suggested by Wynne-Edwards (1929) was apparent.

The failure to detect a correlation requires some consideration, especially since a general method of determining roosting time is involved and also because an essential part of a research report is the planning of future programs. Both persons who made these observations are thoroughly convinced that the starlings roosted earlier on darker days. Indeed this effect was strikingly true on a few stormy days in winter. Also workers in general have the subjective impression that light

TABLE II. *Sample observations of starling roosting*

Time	Nov. 13		Nov. 16		Nov. 20		Nov. 21		Nov. 27		Nov. 28		Dec. 4	
	Star-lings	Photo meter	Star-lings	Photo meter	Star-lings	Photo meter	Star-lings	Photo meter	Star-lings	Photo meter	Star-lings	Photo meter	Star-lings	Photo meter
1520														175
1525													1	210
30													5	200
35		325											5	190
40	3	300											53	160
45	3	250		150						125		105	78	100
50	3	250	0	140		110		110	4	110	2	115	268	75
55	9	230	0	125	6	100	3	100	8	90	15	100	99	60
1600	73	220	21	100	32	95	3	100	19	80	28	90	220	55
05	63	200	72	95	60	95	75	95	125	80	140	80	401	55
10	102	175	60	85	66	90	84	90	39	70	73	70	54	50
15	119	150	148	80	139	80	109	80	171	65	140	65	61	48
20	162	125	167	70	156	75	196	70	282	60	242	60	10	45
25	296	95	213	60	231	60	257	65	114	55	154	55	16	40
30	267	80	90	55	141	55	128	60	67	50	79	50	2	25
35	41	55	129	55	80	55	59	55	20	40	10	43	0	19
40	102	55	17	48	11	50	24	50	6	30	4	27		
45	0	40	4	30	9	37	12	35	0	20	0	19		
50	0	28	0	19	0	19	0	17						
Total	1243		921		931		950		855		887		1273	
Time at 50%		1621		1620		1620		1620		1616		1616		1558
Photom. at 50%		125		70		75		70		65		65		60
Temperature, °F.		54		54		32		36		36		34		60
Minutes before sunset		33		32		29		28		30		29		45

controls roosting time. Hence it seems likely that the difficulty lies in the methods of measurement or analysis rather than the lack of relation.

It will be remembered that the readings were made when the birds arrived and at the place of arrival. But the real stimulus to roosting surely occurs in the afternoon where the bird is feeding. Unfortunately no practical means of determining when a feeding bird leaves for the roost was devised in this study. Perhaps a detailed study of gathering ritual would reveal a method. Another problem is the actual measurement by the photometer. The scale is of course logarithmic but this makes no difference in correlations. But cloud cover alters the readings greatly because white clouds passing over will double the reading regularly. These deficiencies make this approach to the problem very difficult. Another aspect that should be settled is to what extent the same birds roost at the same roost.

The lack of correlation with temperature, humidity or wind is not surprising since these factors probably are not important to a homoiothermic and strong-flying bird.

It is perhaps worth mentioning that the amount of variability is sufficient to make it unlikely that starlings go to roost according to the "internal clock" that is suggested by Kramer (1952) to explain other kinds of behavior.

Morning departure was observed on 15 Saturdays from January 6 to April 21, 1951. The birds began to leave while it was still dark and left in such dense flocks that counts were futile. It was observed that the birds left before sunrise and had all gone by 15 minutes after sunrise.

Unfortunately the data now available do not suggest a generalization concerning roosting time in relation to sunset. The data on starlings here presented are the most complete available and show a rather reasonable change with seasons. But a similar graph for swifts (Haartman 1949) has a very different shape; that for great tits (Dunnett and Hinde 1953, Kluijver 1950) has the opposite trend from the starling data; the "roosting" time for owls (Hansen 1952) is a smooth decline from January to August followed by an increase and Kendeigh (1952: 77) found that wrens extended their activity till after sunset in August when starlings were coming to roost earliest of all. Obviously much more data needs to be accumulated on an annual basis before generalities can be advanced.

SUMMARY

Roosting time of starlings was observed by counting the birds arriving at a building where the birds spent the night in two towers and on vines. A total of 281 counts was made from December 19, 1950 to May 14, 1955. Readings on a photometer showed no correlation with the time before sunset at which 50% of the birds arrived.

This result may merely mean that methods of observation or analysis are inadequate to detect a correlation.

The number of birds in the roost was highest in September, decreased in November, rose again in January and then rapidly declined to a low number in June. The shape of the curve was the same in three winters but the numbers were markedly less in 1952-53.

The birds roosted about half an hour before sunset from November to March, at sunset in April, and almost an hour before sunset in July.

References

Armstrong, E. A. 1954. The behaviour of birds in continuous daylight. Ibis, **96**: 1-30.

Boyd, A. W. 1932. A great Cheshire Starling roost in 1930. Northwest Nat., **7**: 10-18.

Brackbill, Harvey. 1952. Light intensity and waterfowl flight: preflight activities. Wilson Bull., **64**: 242-244.

Brauner, Joseph. 1952. Reactions of poor-wills to light and temperature. Condor, **54**: 152-159.

Brown, F. J. 1946. A Cheshire starling roost, 1944-45. J. Anim. Ecol., **15**: 75-82.

Bullough, W. S. 1942. The reproductive cycles of the British and Continental races of the starling (Sturnus vulgaris L.). Philos. Trans. Roy. Soc. (London), Series B, **231**: 165-246.

Campbell, C. 1902. The starling roost on Grammond Island. Ann. Scot. Nat. Hist., 2-9.

Cruickshank, Allen. 1937. A Long Island bird roost. Proc. Linn. Soc. N. Y., **49**: 68-70.

Cullen, J. M. 1954. The diurnal rhythm of birds in the arctic summer. Ibis, **96**: 31-46.

Cummings, B. F. 1908. Bird roosts and routes. Brit. Birds, **2**: 119.

Dunnett, G. E. and R. A. Hinde. 1953. The winter roosting and awakening behaviour of captive great tits. Brit. J. Anim. Behav., **1**: 91-95.

Elliott, J. S. 1930. The nesting period of the starling. Brit. Birds, **24**: 73-74.

Fitter, R. S. R. 1949. London's Birds. Collins, 256 pp.

Forrest, H. E. 1900. The movements of Starlings. Zoologist: 131.

Franz, J. 1943. Ueber Ernährung und Tagesrhythmus einiger Vögel im Nordfinnland. J. Orn., **91**: 154-165.

Franz, J. 1949. Jahres-und Tagesryhthmus einiger Vögel in Arktischen Winter. Zeit. Tierpsych., **6**: 309-329.

v. Haartman, Lars. 1952. Ueber den Einfluss der Temperatur auf den morgendlichen Gesangsbeginn des Buchfinken *Fringilla c. coelebs* L. Ornis Fennica, **29**: 73-76.

———. 1949. Neue studien über den Tagesrhythmus des Mauerseglers *Apus apus* (L.). Ornis Fennica **26**: 16-24.

Hale, R. W. 1934. Starlings of Herndon District. London Naturalist: 93-95.

Hansen, Lindhard. 1952. Natuglens (*Strix. a. aluco* L.) døgn-og arsrytme. Dansk Ornithol. For. Tidsskr., **46**: 158-172.

Hickey, J. J. 1943. A guide to bird watching. Oxford Univ. Press, 264 pp.

Hinde, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour, Suppl. **2**: 1-201.

Karplus, M. 1952. Bird activity in continuous daylight of arctic summer. Ecology, **33**: 129-134.

Kendeigh, C. S. 1952. Parental care and its evolution in birds. Ill. Biol. Monog., **22**: 1-356.

Kennedy, P. G. 1928. Starlings roosting on the ground. Brit. Birds, **22**: 324.

Kluijver, H. N. 1933. Bijdrage tot de Biologie en de Ecologie van den Spreeuw (*Sturnus vulgaris vulgaris* L.) gedurende zijn Voortplantingstijd. Meded. Platenziektenk. Dienst, Wageningen, **69**: 1-146.

Kluijver, H. N. 1950. Daily routines of the great tit. Ardea, **38**: 99-135.

———. 1951. The population ecology of the great tit, *Parus m. major* L. Ardea, **39**: 1-135.

Koch, J. C. 1930. Jaarverslag 1928/1929 van het "Ringstation Wassenar." Ardea, **19**: 38-62.

Kramer, Gustav. 1952. Experiments on bird orientation. Ibis, **94**: 265-285.

Low, G. C. 1924. Wood pigeons roosting in Hyde Park. Ibis, (6) **11**: 590-591.

MacPherson,, A. H. 1928. A list of the birds of inner London. Brit. Birds, **22**: 222.

Marples, B. J. 1932. Starling roosts and flight-lines near Oxford. Brit. Birds, **25**: 314.

———. 1934. The winter starling roosts of Great Britain 1932-1933. J. Anim. Ecol., **3**: 187-203.

Mayr, E. 1947. A catastrophic decrease in a starling population. Wilson Bull., **59**: 37.

Miller, Loye. 1954. A sparrow hawk's roosting schedule. Condor, **56**: 230.

Morley, A. 1939. Rising and roosting of a pair of resident starlings in winter and early spring. Brit. Birds, **33**: 39-43.

———. 1941. The behaviour of a group of resident British starlings (*Sturnus v. vulgaris* Linn.) from October to March. Naturalist, **788**: 55-61.

Muhlethaler, F. 1952. Beobachtungen am Bergfinken-Schlafplatz bei Thun 1950/51. Ornithol. Beobachter, **49**: 173-182.

Nice, M. M. 1935. Some observations on the behavior of starlings and grackles in relation to light. Auk, **52**: 91-92.

———. 1943. Studies in the life history of the song sparrow. II. Trans. Linn. Soc. N. Y., **4**: 1-328.

Nichols, John T. 1939. Seasonal starling numbers in suburban Long Island. Auk, **56**: 478-479.

Odum, Eugene P. 1942. Annual cycle of the black-capped chickadee. Auk, **59**: 499-531.

Palmgren, Pontus. 1949. On the diurnal rhythm of activity and rest in birds. Ibis, **91**: 561-576.

Pynnönen, A. 1939. Beitrage zur Kenntnis der Biologie finnischer Spechte. II. Ann. Zool. Soc. "Vanamo," **7**: 1-171.

Radford, M. C. 1954. Notes on the winter roosting and behaviour of a pair of nuthatches. Brit. Birds, **47**: 166-168.

Reif, Charles. 1944. Notes on the roosting of the starling. Flicker, **16**: 47-50.

Roebuck, A. 1934. The starling roosts in the East Midlands. Brit. Birds, **27**: 325-332.

Rowan, W. 1938. London starlings and seasonal reproduction in birds. Proc. Zool. Soc. London, (A) **108**: 51-77.

Savage, E. U. 1922. Some observations on the flocking of starlings. Brit. Birds, **16**: 77-78.

Scheer, Georg. 1952. Ueber die Einfluss der Temperatur auf den morgendlichen Gesangsbeginn des Buchfinken in verschiedenen Jahren. Ornis Fennica, **29**: 77-82.

Schwan, A. 1921-22. Ueber die Abhängigkeit des Vögelgesanges von meteorologischen Faktoren, untersucht auf Grund physikalischer Methoden. Verhandl. Orn. Ges. in Bayern, **15**: 9-42.

Seibert, H. C. 1951. Light intensity and the roosting flight of herons in New Jersey. Auk, **68**: 63-74.

Secker, H. L. 1954. Roosting flights of starlings. Emu, **54**: 88-90.

Tischler, F. 1905. Grosse ansammlungen von Staren (*Sturnus vulgaris* L.) zur Brutzeit. Orn. Monats., **13**: 147-149.

———. 1908. Star-Ansammlungen zur Brutzeit. Orn. Monatsber., **16**: 21-26.

Thomson, H. A. R. 1932. The roosts and diurnal distribution of starlings in North Devon during the months December and January 1931-32. Brit. Birds, **26**: 156-160.

Williamson, K. 1947. Field notes on the Faeroe starling. Ibis, **89**: 435-439.

Witherby, H. F. 1929. Breeding starlings resorting to a roost. Brit. Birds, **23**: 187-189.

Woodruffe-Peacock, E. A. 1918. A fox covert study. J. Ecol., **6**: 110-125.

Wynne-Edwards, V. C. 1929. The behavior of starlings in winter. An investigation of the diurnal movements and social roosting habit. Brit. Birds, **23**: 138-153, 170-180.

———. 1931. The behavior of starlings in winter. II. Observations in Somerset. Brit. Birds **24**: 346-353.

SEASONAL DEVELOPMENT IN SUN AND SHADE LEAVES

YOKO O. ANDERSON

Department of Botany, Rutgers, The State University of New Jersey, New Brunswick, New Jersey

INTRODUCTION

It is generally agreed that the same species of plants growing under different environmental conditions often produce leaves that are strikingly different. Light is thought to be one of the most important, if not the chief factor, in producing these leaf differences—hence, the term "sun" leaves for plants growing in full sunlight, in contrast to "shade" leaves for plants growing under less intense light. Wylie (1949, 1951) has demonstrated the occurrence of sun and shade leaves at different locations in the crown of isolated trees by intensively studying differences in tissue volume per unit area of blade and in vein spacings. Although other studies, the results of which are summarized by Burkholder (1936) and Daubenmire (1947), have been made on the ecological anatomy of mature leaves, little work has been done in tracing foliar development of sun and shade leaves from their initial stages in the bud to the fully matured leaf. Consequently, the time and manner in which the characteristic differences arise are not well known. The purpose of this study has, therefore, been to undertake such an investigation and to relate certain environmental factors, namely, temperature and light to the developmental morphology of sun and shade leaves.

The author wishes to express grateful appreciation to Dr. Marion A. Johnson and Dr. Murray F. Buell for their guidance and invaluable assistance throughout the work. Thanks are also due to Dr. John A. Small, who worked in collaboration with Dr. Murray F. Buell, in furnishing the data on light measurements used in this paper.

METHODS

Data reported in this paper have been obtained from *Cornus florida* L. which seems to grow about equally well in full sunlight as in shady woods, and *Viburnum prunifolium* L. which attains maximum vigor and size in open fields. In early October, a fairly mature specimen of each species growing in the dense shade of Mettler's Woods, an oak-hickory forest of central New Jersey, and two other plants of comparable size and age found nearby on an abandoned field of the same soil type as Mettler's Woods were selected for study. Bud or leaf measurements, collections of material for histological examination, and temperature readings were made from October 9, 1952, to July 13, 1953, at approximately monthly intervals in the winter, and at biweekly or weekly visits later in the growing season.

Growth was followed by measuring the length of a series of 5 to 6 vegetative buds along a tagged branch on each plant with a vernier caliper. When this was no longer possible due to the unfolding of the leaves, measurements were made with a mm. ruler. The several buds or pairs of leaves from each branch were averaged to obtain the growth measurements recorded in this paper.

Bud or leaf collections were made by removing a twig close to the median peripheral portions of the plant. The twigs were immediately wrapped

with wet towelling and put into a vasculum. Except for the first few collections when the buds were stored in this condition overnight, the majority of buds and leaves were brought to the laboratory to be fixed within the same day. Buds were descaled, removed from the twigs, and fixed in FAA (5 cc. formaldehyde, 5 cc. glacial acetic acid, 90 cc. of 50% ethyl alcohol). In older leaves, which were always confined to the first pair, small rectangles were removed from the middle of the blade and then fixed in FAA. The leaves from the last two collections were fixed in a formalin-pyrogallol solution (Marengo 1952). The tissues were aspirated, and after fixation they were dehydrated in a n-butyl alcohol series, embedded in paraffin, sectioned transversely with a microtome at 10 microns, and stained with safranin and fast green (Johansen 1940). Serial sections were considered necessary only for the buds.

Temperature records were made with a pair of maximum-minimum thermometers in the woods and with a similar pair in the open field. The thermometers rested on wooden blocks in aluminum shields which were nailed to a post or tree trunk about one meter above ground level. They were oriented so that the bulb pointed in a northerly direction. The thermometers were reset after each reading.

At approximately 1 P.M. on January 17, 1953, a bright cloudless day, light readings were taken with a Weston illumination meter. The photocell was held in a horizontal position about 1.8 m. above the ground. Averages of 36 light readings obtained at 1 m. spacings along a 5 m. square grid were taken in the open, in the woods, and again in the open. The readings which were taken twice in the open were averaged. Further data on light readings for use in this paper were obtained through the courtesy of Dr. M. F. Buell and Dr. J. A. Small.

Results

Growth

There was little growth in both shade and sun leaves of *Cornus florida* and *Viburnum prunifolium* during November, December, January, and most of February. This may be seen in Fig. 1 in which the average length of buds and the average area (length x width) of unfolded blades for the various dates on which they were measured are plotted. Although in both species, the buds of sun plants were slightly longer than those in the shade at the beginning of the experiment, this difference was not considered significant. Early in the experiment, the abandoned field was plowed for cultivation, resulting in the destruction of the sun plants. Buds of sun plants which were newly selected on February 28 were somewhat shorter than buds of the shade plants.

In *Cornus florida,* no change in bud size was observed until about March 30 for the shade plants and April 8 for the sun plants, when significant increases in length occurred as is evident from Fig. 1. Leaves did not begin emerging from their bud scales until two weeks later, April 8 for the shade plant and April 13 for the sun plant. Growth continued at a fairly steady rate so that by April 27, two pairs of leaves from each bud were completely unfolded, and measured an average of 34 mm. long for the shade leaves and 21 mm. for the sun leaves. Although the rate of leaf expansion increased markedly in both *Cornus* plants during the early part of May, the difference of growth rate between sun and shade plants was even more striking, as may be seen by the sharp divergence in their growth curves in Fig. 1. By the first week in June, growth gradually levelled off. At this time the shade leaves of *Cornus florida* were 1.4 times as long and 1.3 times as wide as the sun leaves. The total area of the shade leaves was about 1.9 times greater than that of the sun leaves (Fig. 1).

Bud and leaf growth in *Viburnm prunifolium* followed a similar pattern to that in *Cornus florida.* The buds of *Viburnum* began to show growth considerably earlier, however, as increased bud length measurements in late February indicated. The first pair of shade leaves had completely emerged by the end of March and measured an average of 19.3 mm. in length while sun leaves were only 11.1 mm. long at the time when they emerged two weeks later. Most rapid growth took place throughout April and early May. The final dfifference between the two types of *Viburnum* leaves was even greater than that of *Cornus.* The shade leaves of *Viburnum prunifolium* were 1.5 times as long and 1.5 times as wide as the sun leaves. The total area of the shade leaves was about 2.3 times greater than that of the sun leaves.

In addition to larger size, shade leaves were considerably darker green in color, smoother and thinner in texture than sun leaves in both *Cornus florida* and *Viburnum prunifolium.*

Leaf thickness

Total leaf thickness showed considerable variation in the individual leaves. This may be seen from the sharp dips, which are most frequent at the time of greatest morphological change, in the curves of leaf thickness in Fig. 1. Any decrease in leaf thickness from one date to another was

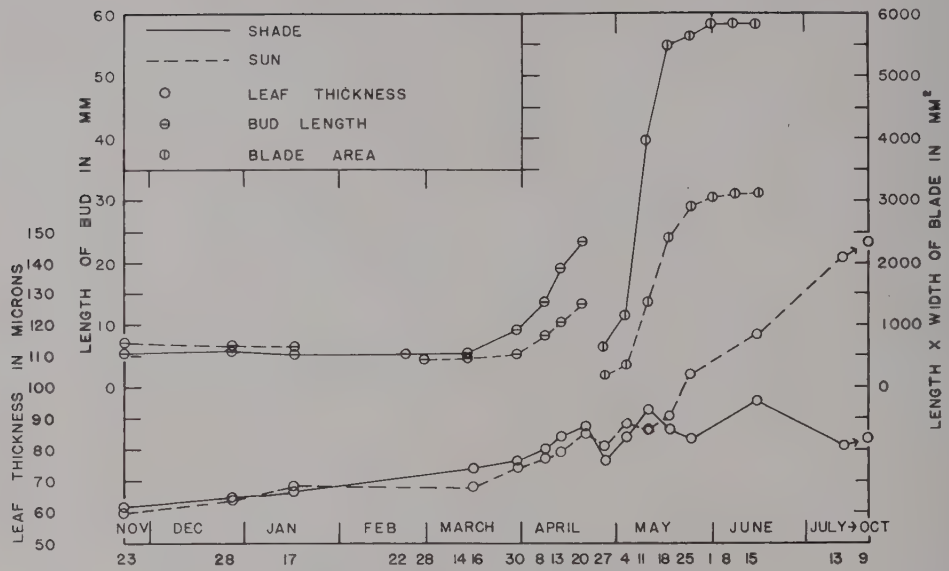

SHADE
SUN
LEAF THICKNESS
BUD LENGTH
BLADE AREA
LEAF THICKNESS IN MICRONS
LENGTH OF BUD IN MM
LENGTH X WIDTH OF BLADE IN MM²
NOV DEC JAN FEB MARCH APRIL MAY JUNE JULY→OCT
23 28 17 22 28 14 16 30 8 13 20 27 4 11 18 25 1 8 15 13 9

FIG. 1. *Cornus florida.* Growth of sun and shade leaves as measured by length of bud and by area (length x width) of unfolded blade. The break in the curve of bud measurements in the sun plant is due to the interval between which the first experimental plant was destroyed and another sun plant was selected for study. The second part of the curve of bud measurements in the sun plant represents, therefore, the averages of an entirely new set of buds.

Leaf thickness of sun and shade leaves. Mature leaves collected on October 9, 1952 were used to compare leaf thickness with leaves collected on July 13, 1953.

probably due to individual variation in the leaves rather than to the method of measurement, since the average standard deviation for the latter was relatively small, ± 2 microns.

About May 6 for *Viburnum* and May 16 for *Cornus*, the rate of increase in thickness for sun leaves began to exceed those in the shade to such an extent that by July 13 leaf thickness had become obviously greater in sun leaves. Shade and sun leaves for *Cornus* had increased 19.9 microns and 89.4 microns, respectively, from the earliest buds collected to the completely mature leaf, while for *Viburnum* the increases were 45.3 microns for shade leaves and 113.9 microns for sun leaves. Comparison of blade thickness in leaves collected on July 13 with that in leaves collected on October 9 of the previous year indicated that significant increases did not occur in either *Cornus* or *Viburnum* after July 13.

A comparison of the thickness or height of the different cell layers was made between "embryonic" and mature leaves as one of the methods in determining the manner in which the layers contribute to the over-all thickness of the leaf. Leaves referred to as "embryonic" were from fall and winter buds in which some differentiation had already occurred, as will be described later. Early stages in primordia development are not considered here. There was an increase in thickness in all layers, except the lower epidermis, in shade as well as in sun leaves with the approach toward maturity. However, the total thickness of sun leaves, which was greater at maturity than that of shade leaves in about the same proportion in the two species, was due to a *relatively* larger increase of cell layer thickness. The palisade, in which marked elongation occurred, was the most important layer in producing this effect. Increased height of spongy mesophyll and upper epidermis also contributed to the final difference, but to a lesser extent. The cells of the lower epidermis measured the same in all four plants both in embryonic and mature stages.

Since the thickness of a leaf depends not only on the height but on the number of cell layers as well, an attempt was made to determine whether there was any significant difference in this respect between embryonic and mature leaves and between sun and shade leaves. In *Cornus florida*, the embryonic leaf consisted typically of 6 layers. However, in some places it was possible to count 7 layers due to additional periclinal divisions in the first layer of the spongy mesophyll. The numerous and closely spaced veins may have been

responsible for this, since increased number of cell layers is usually associated with vein formation. The primarily 6-layered condition persisted throughout the bud stage. In early April, when the leaf cells were undergoing rapid division and cytological changes, 7 layers became as common as 6. In the later collections and in mature leaves, 7 layers predominated, and although intercellular spaces interfered with accurate counting, there were places along the lamina which seemed to consist of 8 layers. There was no apparent difference between sun and shade leaves in the number of cell layers in a comparable stage of development.

The development of cell layers in *Viburnum prunifolium* was similar to that of *Cornus*, except for one additional layer of mesophyll. As in the dogwood, embryonic leaves consisted of 6 layers, although 7 were quite common since there was a great abundance of periclines in the first spongy mesophyll layer. The 7-layered condition became increasingly noticeable after the emergence of the leaves. During the rapid expansion of the leaf, both 7 and 8 layers (4 or 5 layers of spongy mesophyll) were present. In the final stages, 8 to 9 layers were most common, with sun and shade leaves alike.

Internal structure

Changes in the internal structure of sun and shade leaves at various stages of development were observed primarily in regard to the size, shape, and staining intensity of the cells. Although shade and sun leaves underwent the same general morphological changes during their development, the differences arose principally in the time at which the processes were initiated and the extent to which they were carried out. Most rapid changes in cellular structure coincided with the time when rapid growth and increased leaf thickness were recorded. The embryonic leaves remained in much the same condition for both leaf types and for both species from the time when the buds were first collected in early October to the time when the splitting of the bud scales occurred in March and April.

Cornus florida.—In *Cornus florida*, the embryonic leaves lay folded lengthwise along the midrib with their adaxial surfaces facing each other, so that one half of each blade was inserted between the folded blade of its mate. Veins formed from periclinal divisions in the upper layers of the spongy mesophyll were abundant and close to one another. Three or four major veins, many of which contained well-lignified xylem, were conspicuous along either side of the prominent midrib. Illustrations of the embryonic leaves in Figures 2 and 3 show that the cells of the epidermal and two inner rows of spongy mesophyll layers were similar in size and shape and in having large nuclei and dense cytoplasm. In contrast to the cells just described, those of the palisade and last layer of spongy mesophyll layers were considerably larger and highly vacuolate. A conspicuous mass of cytoplasm surrounded the nuclei in these highly vacuolate cells and stained so intensely with safranin that the nuclei were obscured.

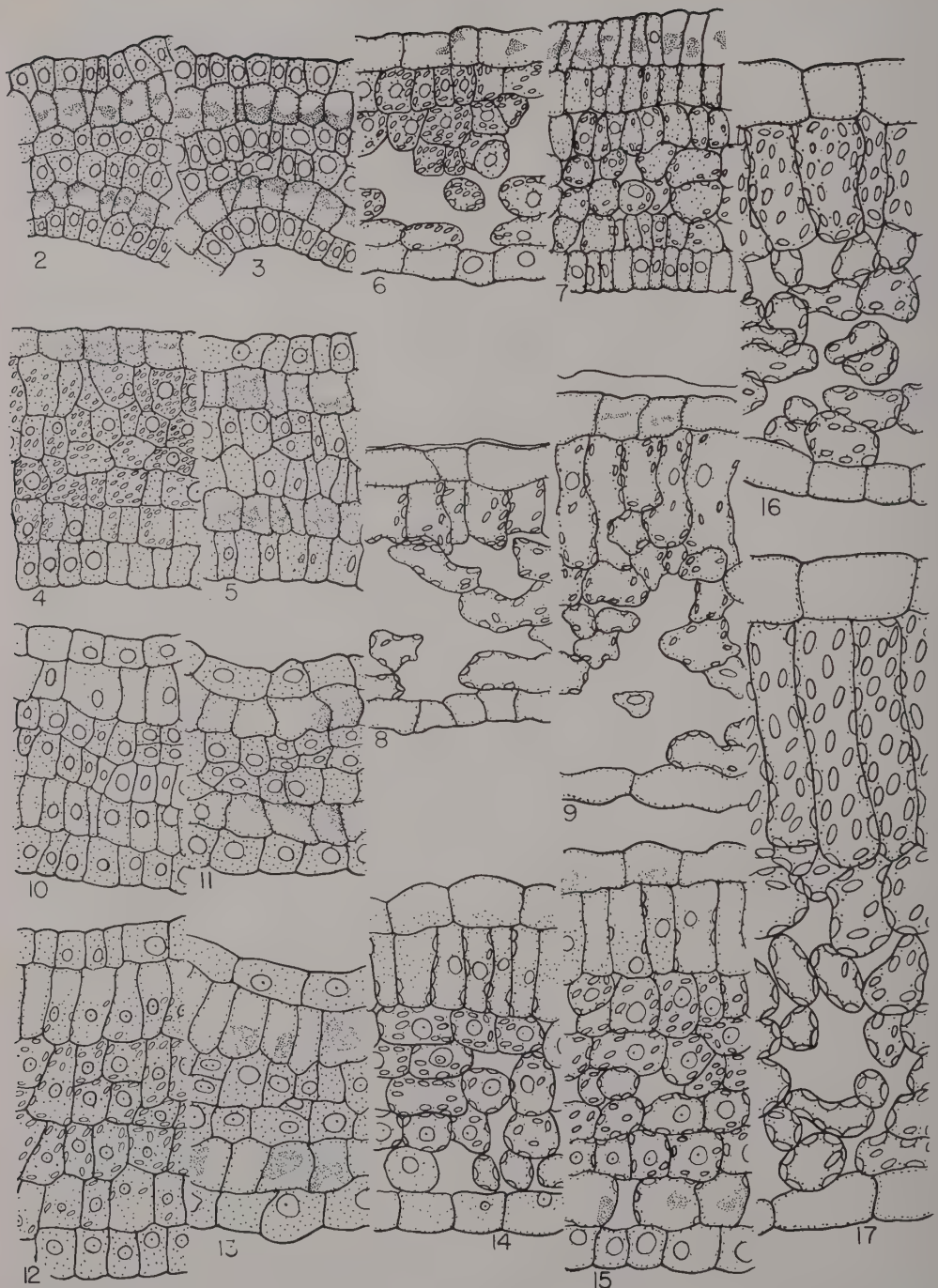
No change was noted from this condition in the shade leaves until March 16 when mitotic figures had become abundant and the staining intensity of the palisade and lower mesophyll layers had decreased. Cell divisions were primarily anticlinal although the first layer of spongy mesophyll had often doubled, as mentioned before.

In the shade leaves of March 30, the submarginal cells had lost their densely cytoplasmic appearance and had become similar to the vacuolate cells of the palisade and lower layer of the spongy mesophyll.

Shade leaves collected on April 13 were the first to show early stages in cellular configuration and differentiation which would later characterize the mature leaf (Fig. 4). The majority of the cells were densely cytoplasmic, except for those of the upper epidermis in which conspicuous vacuolation had taken place. Chloroplasts were recognized for the first time at this date. Although the shape of the cells remained approximately the same, there had been an increase in cell size as well as an enormous multiplication of cells between veins. Cells of leaves collected previous to April 13 had been closely compact, but now occasional intercellular spaces among the spongy mesophyll were found for the first time.

Not until April 27 did the cells typical of the mature leaf appear in the shade plants. The upper and lower epidermal cells had broadened and vacuolated considerably by this time as may be seen in Figure 6. The spongy mesophyll cells had also lengthened in a horizontal direction and their corners had become less angular as they were pulled apart, producing large intercellular spaces. The cells beneath the upper epidermis had assumed the characteristics of a distinct palisade layer. The majority of cells had enlarged and vacuolated to such an extent that the cytoplasm was largely confined to the periphery. Chloroplasts had become abundant in both palisade and spongy mesophyll layers.

Except for larger intercellular spaces and cellular enlargement, mature leaves of July 13 (Fig. 8) did not appear to be considerably different from those collected on April 27 (Fig. 6).



FIGS. 2-9. *Cornus florida.* FIGS. 10-17. *Virburnum prunifolium.* Transverse sections of developing leaves. Dark stippling represents shrunken cytoplasm which is stained intensely red so that the nuclei are obscured. Light-

Sun leaves lagged in their development about one or two weeks behind those in the shade. Thus, the cells of the sun leaves were still typical of those of embryonic leaves on April 13 (Fig. 5) though they had become somewhat larger than in earlier collections. The submarginal cells, however, had become vacuolate on April 8 so that they became continuous in appearance with the highly vacuolate subepidermal cells. Small intercellular spaces and increase in vacuolation in some of the upper epidermal cells did not appear in sun leaves until April 20. In this collection, the nuclei of the conspicuously vacuolated cells did not stain as intensely as in some of the earlier leaves.

Sun leaves of April 27 (Fig. 7) had elongated palisades and conspicuous chloroplasts. The cells had become quite vacuolate and the cytoplasm and chloroplasts stained dark red. In contrast to the shade leaves of April 27, the intercellular spaces were considerably smaller, however. Indeed, it was not until May 11 that the intercellular spaces had become large and conspicuous, and the epidermal cells had broadened out to their mature state. Otherwise, further important changes did not occur in the later collections of sun leaves, except for continued elongation of the palisade cells and the development of a thick cuticle, as comparison with the mature leaf in Fig. 9 shows.

Viburnum prunifolium.—Leaf vernation in *Viburnum prunifolium* was involute with an average of 2 to 3 pairs of decussately arranged leaves within the bud. Except for the midrib, the major veins of these embryonic leaves were less prominent than those of *Cornus florida*. Cellular detail was, however, remarkably similar as Figs. 10 and 11 show. However, the vacuolate subepidermal cells did not continue as far out to the margins as in *Cornus* leaves but were replaced by the densely cytoplasmic cells of the submarginal meristem. A difference between sun and shade leaves in staining intensity was evident in the very darkly stained nuclei of the embryonic sun leaves in contrast to the lighter staining nuclei in shade leaves.

Early stages in differentiation corresponding to those that had occurred in the shade leaves of *Cornus florida* on April 13 were first observed in *Viburnum prunifolium* on March 16. In this latter collection (Fig. 12), the palisade and last layer of spongy mesophyll had become less vacuolate than previously. Chloroplasts appeared to be present, and the palisade cells had elongated to such an extent that they were easily recognized as such.

Definite chloroplasts were seen in shade leaves collected on March 30. The epidermal cells, especially the upper ones, had broadened and vacuolated by this time. The submarginal cells had also become highly vacuolate.

The configuration of the cells as seen in transverse view of shade leaves collected on April 8 appeared to be that of mature leaves. However, extensive cell enlargement and the formation of intercellular spaces continued to occur in older leaves (Fig. 16).

The sun leaves collected on March 16 (Fig. 13) were still in a relatively embryonic condition at the time that shade leaves, which were collected on the same day (Fig. 12), were undergoing conspicuous differentiation. However, the sun leaves rapidly overtook the shade leaves, so that by April 8, sun and shade leaves were not unlike in morphological stucture (compare Figs. 14 and 15). The first sun leaves to show marked differentiation were those of March 30—the extent of development being almost identical to that of shade leaves collected on March 16. Definite chloroplasts and conspicuous vacuolation in the submarginal layer had occurred by April 8 for the sun leaves (Fig. 15). As in the shade leaves, there was little difference between April 8 and the last collection made on July 13 in cell shape or content, though cell size and intercellular spaces

er stippling is used to indicate less intensely stained cytoplasm. X520. Figs. 2, 3. Embryonic shade and sun leaves respectively, collected on October 9. Note the highly vacuolated cells in the subepidermal layers. Epidermal and inner mesophyll layers are densely cytoplasmic. Figs. 4, 5. Emerging shade and sun leaves respectively, collected on April 13. Note that in contrast to the sun leaf which still remains in a relatively embryonic condition, the shade leaf has differentiated to the extent that the upper epidermis is conspicuously vaculolate and chloroplasts are recognizable. Figs. 6, 7. Completely unfolded shade and sun leaves respectively, collected on April 27. Cells are vacuolate in both leaves but the sun leaf has considerably smaller intercellular spaces. Figs. 8, 9. Mature shade and sun leaves respectively, collected on July 13. Greater blade thickness in the sun leaf, due chiefly to the marked elongation of the cells and thicker cuticle, is evident. Figs. 10, 11. Embryonic shade and sun leaves respectively, collected on November 23. The cytoplasm of the subepidermal layers in the shade leaf is somewhat lighter in staining intensity than in the other embryonic leaves. Figs. 12, 13. Emerging shade and sun leaves respectively, collected on March 16. Note that the cells of the shade leaf are undergoing noticeable differentiation while those of the sun leaf are still embryonic in appearance. Figs. 14, 15. Completely emerged shade and sun leaves respectively, collected on April 8. Both leaves appear to consist of mature cells. The shade leaf shows less intercellular space and there are remnants of the intensely staining cytoplasm in the last row of spongy mesophyll. Figs. 16, 17. Mature shade and sun leaves respectively, collected on July 13. Cell elongation, especially in the palisade layer, is evidently responsible for the considerably thicker lamina in the sun leaf.

were considerably larger in the fully matured leaves (compare Figs. 15 and 17).

Upper epidermis

Paradermal examination revealed differences in size and shape in the upper epidermal cells between sun and shade leaves of *Cornus florida* as the series of drawings in Figures 18-25 show. This difference corresponded to the time and extent to which growth in leaf area occurred in the two types of plants. The contrast between the epidermal cells of sun leaves and those of shade leaves was most striking on May 4 (Figs. 20 and 21). At this time, their slightly larger size and waviness in the shade leaf, which had been noticed on April 27 (Figs. 18 and 19), had become greatly exaggerated. Epidermal cells of sun leaves collected on May 11 (Fig. 23) were not as small and as angular as those from earlier sun leaves. By June 15 (Figs. 24 and 25), the difference between the two leaf types had diminished although the epidermal cells of the sun leaves continued to be smaller and less contorted in shape than those of shade leaves.

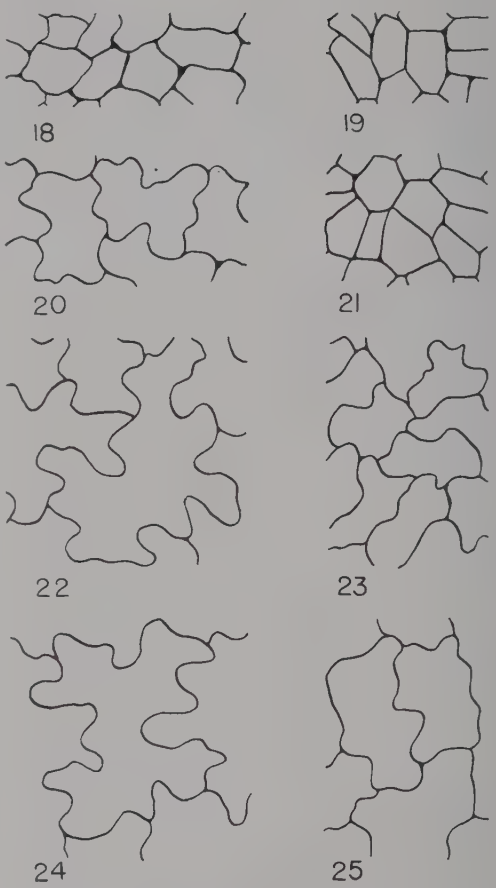
Temperature

The minimum temperature in the woods was generally higher and the maximum temperature generally lower than corresponding temperatures in the open. While the differences varied from 0 to 11.6° F., the minimum temperature in the woods was 6.3° F. higher on the average than that in the open, and the average difference in maximum temperatures between the two areas was 6.5° F.

There was little difference in mean temperature between open and wooded conditions. The mean temperature in the woods was slightly higher during most of the cooler months, however. Although there was fluctuation from one date to another there was a gradual upward trend in all temperature readings with the approach of spring.

Light

The light reaching the 1.8 m. level in Metter's Woods on January 17, 1953, was 44.9% of that of maximum sunlight in the open field. Light readings taken on December 13, 1950 by Buell and Small yielded a similar result, 44.8%. The recorded light readings in the spring of 1950, April 22, as the angle of incidence of the sun increased, thus decreasing the amount of light intercepted by branches and tree trunks, resulted in a relatively high figure of 67.6%. All during the month of May, there was a rapid decline from this percentage of light penetration, with a gradual levelling off in June and July. By July 21, the typical figure for light penetration through a completely foliated deciduous forest was reached—about 3%.



FIGS. 18-25. *Cornus florida*. Paradermal views of the upper epidermis. X520. FIGS. 18, 19. Shade and sun leaves respectively, collected on April 27. FIGS. 20, 21. Shade and sun leaves respectively, collected on May 4. FIGS. 22, 23. Shade and sun leaves respectively, collected on May 11. FIGS. 24, 25. Shade and sun leaves respectively, collected on June 15. Note that the cells of the sun leaf remain relatively small and regular in shape while those of the shade leaf increase in cell size and in waviness of outline to a marked extent and at a greater rate.

DISCUSSION

There is a gradual increase in growth in the winter buds of *Cornus florida* and *Viburnum prunifolium* during March after a winter period of relatively little growth, and then a rapid advance in April, as curves plotted from the growth measurements seem to indicate. Similar growth curves were obtained by Moore (1909) who studied the

winter buds of the common tree and shrub species of Massachusetts.

One of the few papers concerned with the anatomy of the embryonic leaf is that by Smith (1934) who made an intensive study of about 20 common deciduous trees and shrubs. He concludes that embryonic leaves consist of ". . . densely protoplasmic parenchymatous cells which are of uniform size." He notes that cells of *Cornus florida* dissected in April which presented a typically embryonic structure were 6-layered and similar in size and shape and closely compact. The present study of *Cornus florida* and *Viburnum prunifolium* does not completely agree with his observations, however. In the embryonic leaves of both species, the cells are not all alike in size, shape, and staining intensity but are arranged in distinctive layers. The upper and lower subepidermal layers consist of large, highly vacuolate cells and darkly staining nuclei, in contrast to the epidermal and innermost cells which are smaller and more densely cytoplasmic.

Growth of shade leaves of *Cornus florida* and *Viburnum prunifolium* begins earlier in the spring and is manifested by more rapid increases in bud length and by general changes in internal structure one or two weeks in advance of sun leaves. Nordhausen (1903) also observed that buds of shade branches taken from the interior of the crown of trees begin earlier growth than sun buds. However, Watson (1942) states that sun leaves of *Hedera helix* completed their development in 4 weeks while shade leaves did not finish until 11 weeks.

Shade leaves of *Cornus florida* and *Viburnum prunifolium* were also found to be larger in area than those growing under full sunlight. Paradermal views show that the epidermal cells of these shade leaves are not only more distorted in shape but considerably larger. Shank (1938) also observed that shade leaves of *Corunus florida* were larger in size than sun leaves. Isanogle (1944), on the contrary, obtained a smaller area from *Cornus florida rubra* and *Acer platanoides* shade leaves. Her experiment was based on shading to varying degrees one bud from each pair of opposite buds on a twig. Besides the difference in total leaf area, the size and shape of the epidermal cells as recorded by her do not agree with those of the present investigation. She observed that the epidermal cells of the shade leaves were smaller and there were more cells in a given area than sun leaves. Hanson (1917), Clements (1904), and Bergen (1904), all of whom considered a wide variety of species also noted that leaves of plants growing under reduced light were larger in every case. Although greater area was also obtained from shade leaves in such plants as *Renanthera* (Groom 1893), tobacco (Hasselbring 1914) and castor bean (Penfound 1932), there have been other studies made which indicate that sun leaves are larger in *Cucumis* (Gregory 1928) and *Cornus stolonifera* (Marsh 1941). Whether the maximum size attained is greater for shade or for sun leaves, therefore, remains an open question, subject to differences in species and in methods employed by the various investigators.

Mature sun leaves of *Cornus florida* and *Viburnum prunifolium* are definitetly thicker than mature shade leaves. Since there is not a significant difference in the number of cell layers between the two leaf types, thickness in these two species, at least, is contributed mainly by vertical cell elongation. Similar results were obtained by Isanogle (1944) using *Cornus florida rubra* and *Acer platanoides*. In some plants, however, such as *Helianthus* (Clements and Long 1935) and *Pistacia lenticcus* (Bergen 1904) a doubling of the palisade layer has been observed in sun leaves. Smith (1934) is of the opinion that while the mature shade leaf retains the same number of cell layers characteristically found in the embryonic condition, the mature sun leaf may have a greater number of layers than originally.

There is little apparent difference between embryonic sun and embryonic shade leaves of *Cornus* and *Viburnum*. Sun and shade characters are present in mature leaves probably in response to differences in the environment. Cormack and Gorham (1953) found that mature leaves of *Menziesia glabella* and *Lonicera glaucescens* developed sun and shade characters corresponding to the environment in which the leaves expanded and matured rather than to the environment in which their buds developed. Nordhausen (1903) believed that sun and shade characters are already predetermined in the bud. He observed the development of leaves from sun and shade buds by keeping twigs cut from beech plants immersed in water. Sun and shade leaves retained their characteristic features even though shade buds were allowed to develop in full sunlight while sun buds developed in the shade.

The importance of light as a factor in determining sun and shade characters is a well-known fact. Less attention is generally paid to other factors which may be equally or more important in a study of this type where the plants are not grown under controlled laboratory conditions. Temperature differences between the woods and the open field may be important in determining the differ-

ences between sun and shade plants in the time at which leaf development is initiated. The narrower range in maximum and in minimum temperatures as well as a generally hgher mean temperature in the woods may influence the early growth of shade leaves. This belief is largely based on the findings of Gregory (1928) who thought that the unfolding of the first foliage leaves at suboptimal (70.8° F.) levels is controlled largely by temperature. He also demonstrated that temperatures above the optimum (76.8° F.) inhibit cell division in the leaf primordia and there is a decline in rate of growth accompanying supraoptimal (90.3° F.) temperature increases. The smaller leaf area of both species in the present investigation may possibly be due to exposure of the plants growing under direct insolation to supraoptimal temperatures.

Although soil moisture conditions were not considered here, a number of workers (Clements and Long 1935, Penfound 1932, Bergen 1904, Hasselbring 1914) have shown that there is often a close relationship between this environmental factor and plant structure. Plants growing in their natural habitat are continually being subjected to a complex of environmental factors. Therefore the differences observed in plants of the same species growing in different environments can best be understood by analyzing the effect of each factor individually and by varying the factors in as many different combinations as possible. Further research in following the developmental sequence in sun and shade leaves should thus be made in the laboratory under controlled conditions and in the field where as many different environmental factors as possible should be measured.

Summary

1. The development of sun and shade leaves of *Cornus florida* and *Viburnum prunifolium* growing under contrasting light intensities was studied for differences in growth, thickness, and morphological structure. Temperature and light conditions in Mettler's Woods and in an open field, where the plants were found to occur, were compared.

2. Leaves of *Viburnum* emerged and unfolded earlier than those of *Cornus* in the spring. In both species, larger leaf area, which was produced by earlier and larger increases in growth rate (especially at the time of most rapid leaf expansion), was attained by shade leaves.

3. Mature sun leaves were considerably thicker than mature shade leaves. Sun and shade leaves increased in thickness in about the same proportions during the period of early growth increments. The greatest divergence between leaf thickness in the two leaf types occurred later than the corresponding differences in leaf area.

4. Cell elongation, especially that of the palisade tissue, was found to be responsible for increases in blade thickness. There was no difference in the number of cell layers between sun and shade leaves, though it was greater in the mature rather than in the embryonic leaf.

5. Embryonic leaves of sun and shade plants were basically alike in cell structure. The palisade and lowest spongy mesophyll were distinctly different from other layers. Changes in vacuolation of the embryonic cells were most marked during the time of leaf emergence and unfolding. Chloroplasts were also recognizable at this time. The initiation and formation of cells characteristic of the mature leaf was decidedly earlier in shade leaves, as was the case for increase in bud length and leaf expansion.

6. Paradermal views showed the cells of the upper epidermis in shade leaves to be considerably larger and more distorted in shape than those in sun leaves.

7. The drastic reduction of light penetration during and after the canopy had closed in the woods was associated closely with the appearance of differences between sun and shade leaves in blade thickness.

8. Temperature, which was on the average higher and less extreme in the woods, may be one of the determining factors in producing earlier development in shade rather than sun leaves.

References

Bergen, J. Y. 1904. Transpiration of sun leaves and shade leaves of *Olea europea* and other broad-leaved evergreens. Bot. Gaz. **38**: 285-296.

Burkholder, P. R. 1936. The role of light in the life of plants. Bot. Rev. **2**: 97-172.

Clements, E. S. 1904. The relation of leaf structure to physical factors. Trans. Amer. Micro. Soc. **26**: 19-20.

Clements, F. E., and F. L. Long. 1935. Further studies of elongation and expansion in *Helianthus* phytometers. Plant Physiol. **10**: 637-660.

Cormack, R. G. H., and A. L. Gorham. 1953. Effects of exposure to direct sunlight upon the development of leaf structure of two deciduous shrub species. Canad. Jour. Bot. **31**: 537-541.

Daubenmire, R. F. 1947. Plants and environment. John Wiley & Sons, Inc., New York. 424 p.

Gregory, F. G. 1928. Studies in the energy relations of plants. II. The effect of temperature on the increased area of leaf surface and dry weight of *Cucumis sativis*. Ann. Bot. **42**: 469-507.

Groom, P. 1893. The influence of external conditions upon the forms of leaves. Ann. Bot. **7**: 152-153.

Hanson, H. C. 1917. Leaf structure as related to environment. Amer. Jour. Bot. **4**: 533-560.

Hasselbring, H. 1914. The effect of shading on the transpiration and assimilation of the tobacco plant in Cuba. Bot. Gaz. **57**: 257-286.

Isanogle, I. T. 1944. Effects of controlled shading upon the development of leaf structure in two deciduous tree species. Ecology **25**: 404-413.
Johansen, D. A. 1940. Plant microtechnique. McGraw-Hill Book Co., New York. 523 p.
Marenge, N. P. 1952. Formalin-pyrogallol as a fixative for plant cytoplasm. Stain Techn. **27**: 209-211.
Marsh, F. L. 1941. Water content and osmotic pressure of sun and shade leaves of certain woody prairie plants. Bot. Gaz. **102**: 812-815.
Moore, E. 1909. The study of winter buds with reference to their growth and leaf content. Bull. Torr. Bot. Club. **36**: 117-145.
Nordhausen, M. 1903. Über Sonnen und Schattenblätter. Ber. deutsch. Bot. Ges. **21**: 27-45.
Penfound, W. T. 1932. The anatomy of the castor bean as conditioned by light intensity and soil moisture Amer. Jour. Bot. **19**: 538-546.
Shank, C. K. 1938. The leaf and stem anatomy of *Cornus florida* in relation to light exposure. Amer. Midl. Nat. **19**: 417-426.
Smith, G. H. 1934. Anatomy of the embryonic leaf. Amer. Jour. Bot. **21**: 194-209.
Watson, R. W. 1942. The mechanism of elongation in palisade cells. New Phytologist **41**: 206-221.
Wylie, R. B. 1949. Differences in foliar organization among leaves from four locations in the crown of an isolated tree (*Acer platanoides*). Proc. Iowa Acad. Sci. **56**: 189-198.
———. 1951. Principles of foliar organization shown by sun-shade leaves from ten species of deciduous dicotyledonous trees. Amer. Jour. Bot. **38**: 355-361.

THE SEASONAL LIFE HISTORY OF DAPHNIA IN AN ARCTIC LAKE

W. T. Edmondson
Department of Zoology, University of Washington, Seattle, Washington

Introduction

The purpose of the present paper is to discuss in some detail the population of Daphnia in Imikpuk, a shallow lake near the Arctic Research Laboratory, Point Barrow, Alaska. Of the planktonic animals present, *D. pulex* var. *tenebrosa* Sars 1898 is the most important in terms of bulk, although two others are much more numerous. The material consists of quantitative samples taken on 11 dates in 1951 and 30 dates in 1952, and some additional qualitative samples. This is one of a number of papers being prepared on the results of a study of Arctic limnology, a preliminary report of which has been published (Comita and Edmondson 1953). These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Washington, NR 165-080.

The entire responsibility for the conduct of the field work was undertaken by Dr. G. W. Comita, then a graduate student, who served as Chief Scientist on the project. The author is glad to take this opportunity to express his appreciation of Dr. Comita's initiative and painstaking work which was carried through successfully under Arctic conditions, and work in connection with all phases of the project in Seattle.

In the 1951 field work, Dr. Comita was assisted by Mr. Robert A. Main, and in 1952 by Mrs. G. W. Comita. A number of other assistants have contributed to the present paper by making counts, measurements and calculations; to Mr. Curt Wiberg, Mr. Robert Black, Mr. Russell Zimmer, and Mrs. H. E. Broadbooks, the author expresses his thanks for their careful work. Thanks are due others who provided help. Dr. John L. Brooks of Yale University identified the Daphnia, made special examinations of material, and has been very generous with information. Mr. John J. Koranda kindly took plankton samples after the lake had frozen in 1952. Dr. John L. Mohr sent living animals and ephippia in 1954. Mrs. R. G. Merritt helped prepare figures for publication. Special thanks are due Miss Patricia Dudley who made the photographs in Figure 2.

Limnological Conditions

A paper now in preparation will give a detailed discussion of the limnology of Imikpuk. To avoid duplication, only the necessary minimum of general information will be presented here. Imikpuk is approximately elliptical in shape, 1065 meters long, 680 meters wide, with a maximum depth of 2.8 meters. It contains no higher vegetation, but there are areas on the bottom where Vaucheria forms mats. The bottom material near shore is composed of silt and gravel, while the deeper deposits are much softer. Imikpuk is freely exposed to the high winds that blow all summer with varying intensity and direction. (Fig. 1A).

In 1952, when the first sample was taken on July 6, the lake had only partly melted around the edge. It was not possible to take a quantitative sample then nor on July 8, but by July 10 the floating block of ice was small enough to permit launching of the boat and operation of the sampler. The last ice was observed on July 21. During the summer samples were taken frequently, the longest interval being 5 days, until September 21 when the last quantitative sample was taken.

The temperature rose rapidly after the lake

thawed, to a maximum of 10.5°C at the surface (Fig. 1A). Measurements in 1951 showed essentially no difference between surface and bottom temperatures. Ice reappeared about September 25. Mr. Koranda's qualitative samples were taken through holes in the ice on 8 dates through December 1.

The only species of Daphnia in the lake is *Daphnia pulex* var. *tenebrosa*. No other cladoceran is numerous in the plankton. This variety was first described by Sars from the New Siberian Islands in the Arctic, and very likely it has been recorded by others without varietal distinction. There have been no further publications of the name *tenebrosa*. Brooks is preparing a monograph in which he will deal fully with the taxonomic status of the variety. His records show that while it is frequent in the far North, it also occurs in scattered localities outside the Arctic, mostly in the mountains of western North America. The southernmost locality yet known is about 37° N lat. in the Sierra Nevada.

Since the seasonal events in Imikpuk are rather different from those in more familiar lower-latitude lakes and ponds, a brief summary will be given of a usual seasonal history of Daphnia. Populations may winter over as adults or as resistant resting eggs contained in cases, ephippia. The ephippial eggs hatch in favorable conditions and give rise to females that reproduce by parthenogenesis, producing eggs without a chromosomal reduction, and carrying the eggs in a dorsal brood chamber until hatching. These eggs are the "summer eggs" or "parthenogenetic eggs" of various authors, or "subitaneous eggs" of Berg (1931). There are no traces of meiotic processes involved in the production of these eggs. Daphnia thus represents an extreme in the series of reductions of meiotic processes in apomictic parthenogenesis (Mortimer 1936; Suomalainen 1950). There may be a long series of such parthenogenetic generations, the entire population consisting of females. Sex determination in Daphnia is environmental, the parthenogenetic, diploid eggs being capable of developing into either females or males. Eventually, in response to environmental conditions, some of the parthenogenetic eggs develop into males, and some of the females produce eggs with a haploid number of chromosomes. These eggs ordinarily require fertilization to develop. If fertilized, they become enclosed in an ephippium developed from the dorsal part of the carapace. Some authors have referred to these eggs as "sexual eggs," although such usage is undesirable. Conditions for production of males are somewhat different from those for production of ephippial eggs, and populations may persist for some time with a small proportion of males and no ephippia. The ephippial eggs are capable of developing after desiccation and freezing, and are thus well adapted for carrying the population through winter or drought. For reasons that will become apparent, it is inappropriate in *Daphnia pulex* var. *tenebrosa* to describe the ordinary eggs as "parthenogenetic" in contrast to those laid in ephippia. Moreover, since ephippial eggs at least of some species are capable of rapid development, the term "resting egg" in contrast to "subitaneous egg" (Berg 1931) seems inexact. In this paper, the terms *non-ephippial* and *ephippial* will be used to describe the two kinds of egg. An animal carrying an ephippium is referred to as *ephippial*, while an animal that has hatched from an ephippial egg is called *exephippial*. Exephippial animals are always females, although Ekman (1904, p. 88) discussed a possible exception. Exephippial females may produce ephippial eggs in the first brood.

Methods

In 1951 quantitative plankton samples were taken from the surface and from just over the bottom with a three-liter Kemmerer-type water sampler, and poured through a Wisconsin-type plankton net made of no. 25 bolting silk. Usually a total of 30 liters was strained, but on some occasions much more was taken. In 1952 samples were taken with a Clarke-Bumpus quantitative sampler equipped with a no. 20 net (Clarke and Bumpus 1950). All samples were preserved with formalin. The 1952 samples were taken in duplicate in an attempt to eliminate the effect of small-scale patchiness of distribution. The sampler was operated from a 12-foot aluminum boat powered with a 5-horsepower outboard motor. The sampler was slowly raised from the bottom to the surface with the boat in motion to insure adequate sampling of the entire depth of the lake.

Some concern has been expressed about the use of a net as fine as no. 20 with the Clarke-Bumpus sampler (Langford 1953; Clarke and Bumpus 1950). The present author has abandoned the use of the no. 20 net in lakes where there is a sizable phytoplankton population, for when the net clogs, the passage of water through the net is too slow to permit the metering mechanism to operate properly. Nevertheless, it is believed that truly quantitative samples were obtained in Imikpuk. Despite the fact that the Imikpuk phytoplankton population is large relative to other lakes in the region (Prescott 1953), it is sparse by ordinary standards, and evidently did not clog the net appreciably. The number of meter revolu-

tions obtained was satisfactorily large, giving sample volumes from 164 to 780 liters, mean 396, and duplicates agreed very well in most cases. For non-ephippial Daphnia, the average of the deviations from the mean of each pair was only 13% of the mean. Success in using such a fine net depends, in addition to lack of a dense population of clogging organisms, on moving the sampler through the water sufficiently fast to press water through the net rapidly enough to turn the metering mechanism at a rate within the calibration range. The use of an outboard motor of sufficient power is essential for successful use of the no. 20 net.

The instrument was originally calibrated by Dr. Comita who found that 1 revolution represented 4.56 liters of water strained at a flow rate of 14 revolutions per minute. The machine was later re-calibrated by Mr. C. S. Yentsch in an elaborate sluiceway at different rates of flow. The factors varied from 4.44 to 4.36 liters per revolution at flows of 60.3 to 85.0 revolutions per minute. It appears that the sampler has a very satisfactory linearity over an unusually wide range. It should also be noted that a no. 20 net becomes less pervious with age. The net used in Imikpuk had not been used before. At the end of the season, microscopic inspection showed that the condition of the weave had changed little as compared with fresh silk and with an old no. 20 net which had been abandoned because of clogging.

For counting, the material was placed in a plastic tray with lines ruled on the bottom. The entire contents of the tray were counted. When the population was small, the entire sample was counted. When it became so large that counting the entire sample was impracticable, aliquots of about 50% were taken with several operations of a wide-mouthed automatic pipette. Usually the animals counted numbered several hundred. The method used was much like that described by Ricker (1937).

Measurements of Daphnia were made at a magnification of 27x using an ocular micrometer in an eyepiece of a binocular dissecting microscope. The value of the smallest division was 0.034 mm. Measurements were recorded to the nearest division and are given in the text to the nearest 0.01 mm. The animals were placed horizontally, measured from the base of the spine to the top of the head, the measurement corresponding to the "total length" of Anderson (1932), but of course this does not include the spine. This dimension will be referred to as length of animal, or more simply as "length." The length of the spine was also measured, and expressed as a percentage of the length just described.

Results

Seasonal Changes in Population

The total population of all female post-natal stages was very small at the beginning of the sampling period (Fig. 1C). The subsequent development of the population can be described as involving a period of considerable increase to a maximum of about 3500 individuals per cubic meter, with a subsequent decline and an abrupt increase at the end of the period. Superimposed on this general pattern are a number of irregularities which will be discussed in detail. The small changes in July are of the sort that ordinarily might be dismissed as the result of the usual sampling error. Nevertheless, each point represents the average of two samples which were in good agreement, with the exception of July 15, 23, August 1, 5 and 20 when but one sample was taken. The population declines of July 24, 28 and August 5 evidently represent genuine changes of the population in the part of the lake sampled. An analysis of the changes will be presented in a subsequent section.

The early population consisted entirely of small animals. As time passed, increasingly larger animals were collected. At no time were males found. Small, slender animals were subject to close scrutiny, but no features were found to suggest that they were other but young females. Dr. Brooks kindly examined the gonads of such individuals and reported that they contained oōcytes. The complete absence of males from this Arctic population has interesting implications which will be taken up in the Discussion.

For further discussion of seasonal changes, information on reproduction and growth is needed.

Reproduction

Loose ephippia were encountered in most of the early samples, many empty and all having a rather battered appearance. They tended to be lighter in color than freshly produced ones. Obviously, these ephippia had been produced in 1951, and were the source of the small Daphnia. Confirmation was given by the finding in one of the July 10 samples of a Daphnia in embryonic condition, invested in a thin transparent oval membranous bag. The bag lacked the end pieces described for *Daphnia pulex* by Vollmer (1912) (Fig. 2F).

The ephippia of this variety agree well with the description by Olofsson (1918) in having two long cuticular strips from the posterior end, derived

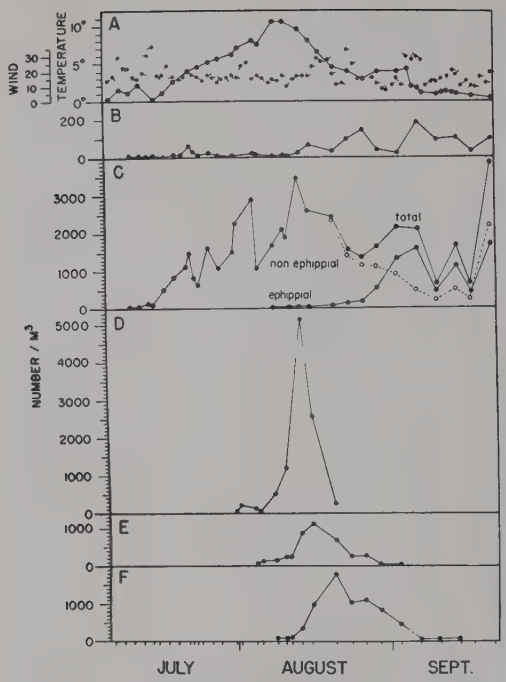


FIG. 1. Wind, temperature and Daphnia population in Imikpuk, 1952. A. Surface temperature of lake in centigrade degrees, connected circles. Wind speed; fastest mile of the day in miles per hour. Prevailing direction is shown by short line extending from circle toward direction from which wind came, with north at top (Data from U. S. Weather Bureau.) B. Loose ephippia. Note that the scale is different from the lower panels of the figure. C. Daphnia; with and without ephippia, and total population. D., E., and F., early, middle and late stage embryos, respectively. The dates shown along the baseline are July 6, 8, 10, 12, 14, 15, 17, 19, 21, 22, 23, 24, 26, 28, 31, August 1, 4, 5, 8, 10, 11, 13, 15, 20, 23, 26, 29, September 2, 6, 10, 14, 17, 21.

FIG. 2. Photographs of Daphnia embryos, stages defined in text. A. early stage. B. early middle stage. C. Late middle stage. D. Early late stage. E. Late late stage. F. Ephippial embryo. Each photograph is marked with a scale 0.1 mm. long. The specimens were mounted in glycerine and show more detail than was visible in uncleared samples during counting.

from the ventral edge of the carapace. The strips seem to break off easily, but many ephippia retained them.

On August 13, the first animals carrying distinct ephippia were collected, the length of the animals varying from 2.45 to 2.72 mm. Some of the ephippia contained two eggs while others were empty. It is a fair presumption that ephippial animals with the ovary not enlarged had produced eggs which had fallen out after preservation. On August 15, animals were found with ephippia and with partly swollen ovaries; probably their eggs had not yet been laid. The same sample contained a number of fresh-looking ephippia with unbroken posterior spines, in contrast to those found earlier.

Previous to the appearance of the first ephippial animal, starting on August 10, specimens were collected which showed a distinct darkening of the dorsal part of the carapace posterior to the region of the fornices. It was thought at first that these animals were about to form ephippia, but later collections contained such animals with non-ephippial eggs in the brood chamber, so the darkening by itself cannot be taken as an indication of incipient ephippium formation. While a characteristic of the variety is a darkening (tenebrosity) of the dorsal part of the carapace, the young specimens in Imikpuk do not have it. Evidently the carapace becomes dark shortly before maturity. Nevertheless, one of the darkened animals in addition showed a double notch in the dorsal profile very much like that shown by ephippium-carrying ani-

mals, and it presumably was about to produce an ephippium. Much later, on August 23, an animal with non-ephippial embryos was observed to have a single indentation. Evidently it is necessary to use care in distinguishing incipient ephippium formation.

In order to determine the time of reproduction, the embryonic stages developing from non-ephippial eggs were counted. The embryos were arbitrarily classed as early, middle and late stages, defined as follows:

Early. (Fig. 2A) Shape round or only slightly elongate. (At first the embryos are nearly spherical, but soon become somewhat flattened. Toward the end of this stage cracks appear which later turn out to mark the separation of the second antennae from the body.)

Middle. (Fig. 2B, C) Elongate, with distinct head bulge. (Early in the stage the second antennae are present as short forked stubs, closely appressed to the body. Later, they become separated, the rami appressed to each other. Toward the end of this period the antennal rami separate and three terminal setae appear which are much shorter than the rami themselves. Thick longitudinal folds become thinned out and grow ventrad to form the carapace while at the posterior end the dorsal spine forms, curled ventrad and anteriad between the posterior edges of the carapace. During this time, the thoracic appendages appear as stubby blocks of tissue.)

Late. (Fig. 2D, E) With well developed eye pigment. (By the time the animals leave the brood chamber, the eye is as dark as that of the adults. Apparently the period of pigment development is short, as there was ordinarily little trouble in deciding whether the eye pigment was "well developed." The oldest late embryos are easily distinguished from the newborn young by the fact that the latter have the terminal antenal setae longer than the rami and the dorsal spine is extended. In newborn animals the spine is usually recurved, but occasionly is crooked.)

The definitions of stages are based on the appearance of the formalin-fixed material under a binocular dissecting microscope at the 9 x magnification used for counting. In specimens cleared with glycerine, the lightly pigmented, double eye primordia are seen in middle stage embryos, and many other details appear which are not visible under the conditions used in counting. No disintegrating embryos were recognized such as have been observed in presumably poorly fed natural populations (Brooks 1946).

It is not intended that the stages as defined above necessarily receive general adoption for use in describing cladoceran populations. Nevertheless, attention should be given in zooplankton work to the entire population, not just the adult stages. With sufficient study it would doubtless be possible to define a greater number of embryonic stages, and to make a finer analysis of the sequence in the population. A well analyzed series corresponding to the normal stages of the amphibian embryologists would be useful (Rugh 1948). The closest thing to a standard series which the author has found is the paper by Obreschkove and Fraser (1940) presenting photographs and descriptions of the gross features of *Daphnia magna* embryos at three hour intervals. Development *in vitro* at 25°C took 46 hours, so the interval between photographed stages represented 6.5% of the total developmental time. As defined above, *early embryos* correspond to approximately the first 24 hours (52%) of development of *Daphnia magna, middle embryos* correspond to the next 6 hours, (13%), and *late embryos* correspond to the last 16 hours (35%). Thus, it is seen that the periods used in this paper do not represent equal time intervals, but the difference is probably not as great as appears. Apparently the time of elongation of the head region which marks the beginning of the "middle stage" occurs earlier in *Daphnia pulex* var. *tenebrosa* than in *D. magna.* The latter species seems to have more development of posterior parts when the head elongates, and it is difficult to find an exact correspondence between the photographs of early stages of *D. magna* and the specimens of *D. pulex* var. *tenebrosa,* although later stages seem to agree fairly well.

Reproduction started sporadically during the last week of July, and became continuous in early August. On July 26, the samples contained two animals with enlarged ovaries. The animals were 1.94 and 2.24 mm. long. Another animal, 2.86 mm. long, had 10 early embryos in the brood chamber. This number of embryos suggests that the food supply was relatively satisfactory. No more embryos were collected until August 1. On July 31, the largest specimens had distinctly enlarged ovaries. These animals ranged in length from 2.31 to 2.38 mm. An animal with partly enlarged ovaries was 2.21 mm. long. On August 1 there were a few animals distinctly larger than the largest present the day before. Two of the specimens had 9 and 18 eggs in the brood chamber, and were 2.69 and 3.06 mm. long respectively. In addition there were loose eggs which had presumably fallen from brood chambers of other an-

imals after preservation. The eggs varied in diameter from 0.27 to 0.31 mm.

If the average clutch size is 14, the maximum number of animals carrying non-ephippial eggs was only about 12% of the total.

Early embryos occurred in all samples through August 20, after which no more were seen (Fig. 1D). The maximum number was collected on August 13. Middle stage embryos occurred in very small numbers on August 4, building up to a maximum on August 15 and not occurring after September 2 (Fig. 1E). Examination of the curve shows that a better estimate of the date of maximum, based on interpolation within the five-day sampling interval, would be about August 17. During the period August 4-20, the development of the largest middle stage embryos was visibly more advanced in each succeeding sample, with the antennae becoming progressively longer, the rami separating and developing three short setae at the tips, the body elongating, and rudiments of thoracic appendages appearing.

On August 10 the first late embryos appeared in small numbers, the pigment in the eye being slightly but definitely developed. The maximum occurred on August 20, and the last one was collected on September 14, although the number of late embryos was very small on and after September 6 (Fig. 1F). During the period leading up to the maximum, the late embryos too exhibited the progress of their development, as the carapace completed growth, the posterior spine lengthened and the postabdomen and appendages took form.

Thus there was one brood of non-ephippial eggs. The maximum number of early stage embryos was somewhat more than twice the sum of the other two stages, although the early stage took only about half the total time of development, at most. Therefore, there must have been a high embryonic mortality early in development. Since disintegrating embryos were not observed, the mortality may be attributed to the death of ovigerous females. The abrupt decline of early embryos from August 13 to August 15, not matched by an equal increase of middle and late stages, coincided with a decline of animals from 3560 to 2610 per cubic meter, an amount ample to account for the disappearance of the embryos. As will be shown below, the dying animals were mostly later, mature instars. It is interesting that ephippial females were found only shortly after the appearance of middle stage embryos (Fig. 1) and became abundant before the new brood reached maturity. This fact must mean that many of the exephippial animals produced ephippia directly. The observation is in accord with laboratory experience (Berg 1931), and with that of Olofsson with Arctic populations (1918). The possibility also exists that some of the animals which produced a brood of non-ephippial eggs later made ephippia.

Instar Analysis

The development of the population of post-brood-chamber stages was analyzed further on the basis of length-frequency distributions. At least 100 animals were measured except in the earlier samples when fewer than 100 were collected. For purposes of presentation (Fig. 3), the data are grouped in histograms so that the width of each bar represents 5 eyepiece micrometer units (0.170 mm.). In the entire set, only one animal was recorded as 20 units long; it has been counted in the 21-25 group.

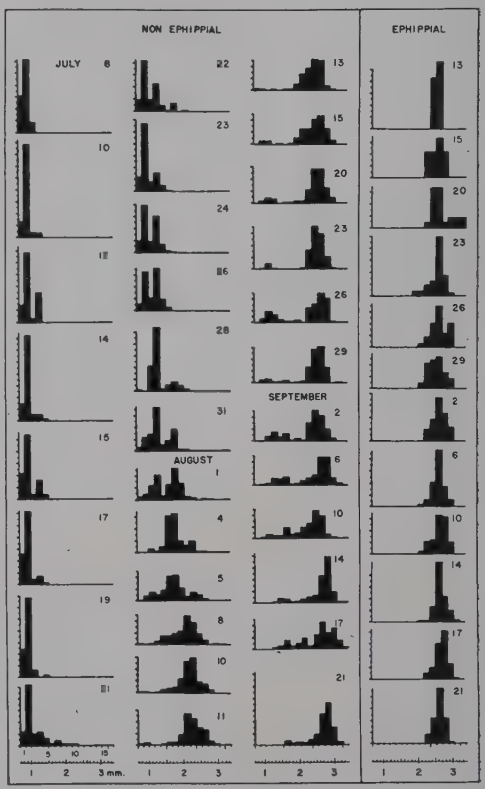


FIG. 3. Length-frequency histograms for each date of collection. Each bar represents 5 micrometer units, or 0.170 mm. The smallest size group shown is 21-25 units, the largest 96-100. A millimeter scale is shown at the bottom of each row. Each graduation on the vertical axes represents 5% frequency. The first three columns represent non-ephippial animals including those which had cast an ephippium. The last column includes animals carrying ephippia at the time of collection.

An examination of the length-frequency histograms for each date (Fig. 3) is very revealing. The sequence July 23-24-26 obviously suggests that the smaller modes represent individual instars. Larger modes are not so clearly separated. The population minimum of July 24 is matched by a disappearance of the larger animals which had been present on July 22. Apparently the rapid recovery of the population resulted from the continued presence of overwintered ephippia, of which there was an increase in the samples on July 22. By August 10 the animals on the whole had shown a marked increase in length, although there were always small animals present. The presence of the small animals seems to be evidence that ephippial eggs continued to hatch during the first half of the summer, possibly as more and more were washed out of the bottom or blown in from the shore. It should be pointed out that in a percentage-frequency histogram, the frequency of one group may decrease either because of an absolute decrease in that group or because of an increase in another group with no change in the first, or even a small increase.

In the middle of August, about a week after the appearance of the first late stage embryo, there appeared a small group of animals which seem to be the offspring of the brood of non-ephippial eggs. The problem of identification of the smallest animals of the new brood and the time of their appearance will be discussed in a subsequent section.

Examination of the histograms shows that a five-unit grouping is too coarse to reveal the details, particularly the later instars. The ungrouped distributions were therefore studied at great length, and nine size groups recognized. It is presumed that these groups represent instars. The first six groups are reasonably well separated, the other three less so. The presence of peaks is clear enough in the ungrouped data, but the exact delimitation between one and another is sometimes obscure. Nevertheless, when there appeared to be no basis in one sample for deciding where two instars were separated, sometimes the earlier and later samples permitted a good separation to be made. After the middle of the season it is necessary to take account of the existence of the growing brood of animals from non-ephippial eggs, each instar of which is probably somewhat different in size from the same numbered instar from ephippial eggs. The mean sizes of the exephippial animals and the new brood are compared in Fig. 4A. It should be noted that the curve for the new brood represents only those animals distinguishable on the basis of size, and therefore does not include fast-growing animals of the new brood which had already achieved adult size. In other words, the curve gives the mean size of animals in the smaller modes in Figure 3. If it had been practicable to include all members of the new brood, the curve would approach that for non-ephippial animals much more closely after the middle of September.

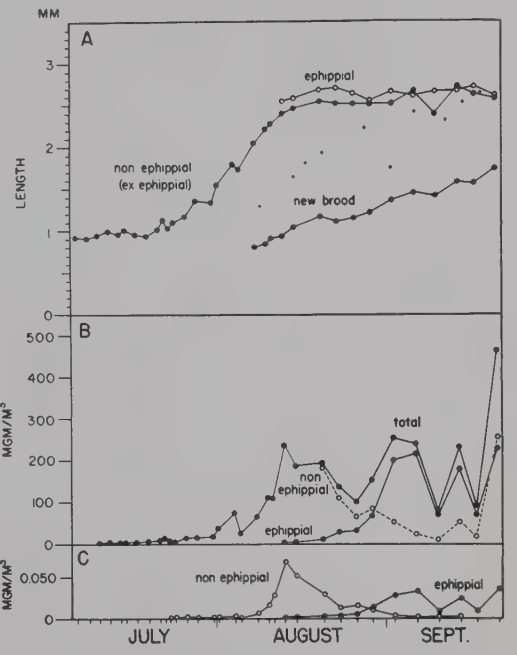


FIG. 4. A. Mean length of non-ephippial animals hatched from ephippial eggs, of ephippial animals, and of the new brood of animals hatched from non-ephippial eggs. The small unconnected points represent non-ephippial animals collected in 1951. B. Mass of Daphnia population not including eggs. This graph corresponds to Panel C of Fig. 1. C. Mass of eggs carried by the animals shown in Panel B.

The percentage-frequencies of the nine size groups and total population size were used to calculate the actual population density of each group (Fig. 5), since it is desirable to put the numbers on an absolute basis as well as a comparative one. In this calculation no attempt was made to separate the animals derived from the two types of eggs, for, as will be seen, there was little overlap of occurrence of the smaller sizes.

A study of the data of Figures 3 and 5 shows that there must have been a heavy mortality of the non-ephippial embryos at the time of hatching, for from about 1800 late stage embryos per cubic meter only about 300 first instar animals resulted, and mortality evidently reduced the later instars even further. The length-frequency histograms for the period August 20 to September 14 show what a small fraction of the total population was

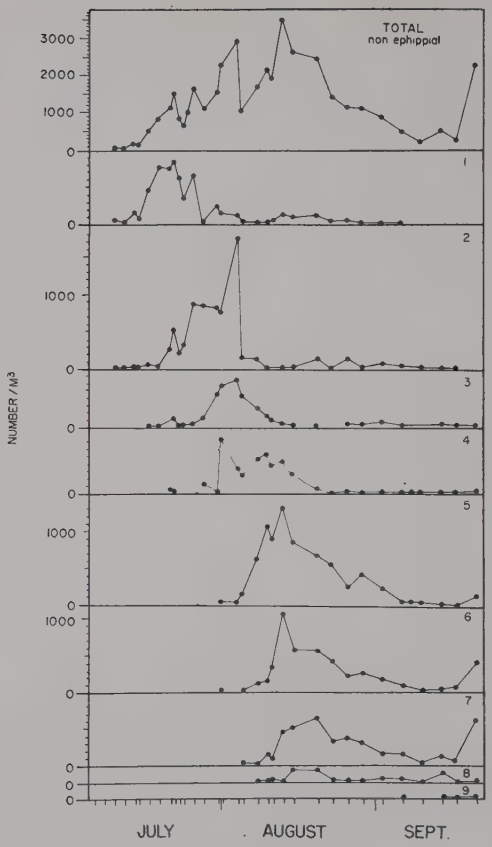


FIG. 5. Abundance of the nine size groups, presumed to be instars of non-ephippial Daphnia, and total.

made up by the new brood of animals produced from non-ephippial embryos. Obviously, non-ephippial eggs do not maintain the species in Imikpuk, if the year 1952 is representative of the usual reproductive events.

Change in Population Size

On the basis of the instar analysis it is possible to understand the small population minima of July 24 and 28 as resulting from death of particular instars. On July 22, the first four instars were present, the fourth being represented by very few individuals. By the 23rd, all had dropped, the 4th disappearing completely, and the percentage change being greatest in the third, less in the smaller instars. By July 24, Instars 2 and 3 had shown an increase, but Instar 1 had dropped still further. The abrupt drop of Instar 1 between July 26 and 28 without increase in Instar 2 suggests high mortality of 1. The fact that Instar 3 increased afterwards shows that there must have been continued hatching of ephippia. When the duration of changes is short in relation to the sampling interval, it is not possible to find every change in one stage preceded and followed by changes in precedent and subsequent stages. In any case, the data have to be interpreted as resulting from processes adding to and taking from the standing crop at the moment. The change in one stage will be determined not only by how fast members are lost by death and by metamorphosis to next stage, but by recruitment from the next earlier stage. Thus, as in this case, two odd-numbered stages may show a sequence that shows only vaguely in the interposed even-numbered stage. The very sharp drop of August 4-5 is largely attributed to second instar animals, the fourth instar having decreased previously. Of course the probability of sampling the rarer large animals is less than that of catching the smaller animals, but the size of the samples and consistency of changes makes this interpretation reasonable.

The total population increased in size until August 13 when it was slightly larger than on August 4. If this increase is genuine, it must have resulted from continued hatching of ephippial eggs, since the non-ephippial embryos had not developed far enough to provide the new animals (Fig. 1). The continued presence of early instars during the period of increase is consistent with this explanation, but since there was no progession of successive maxima of the early instars, it must be supposed that each instar was losing numbers by metamorphosis to the next instar about as fast as it was gaining numbers from the earlier instar. The lake was much warmer during this period than it was during the first increase early in July. The possibility must be considered that horizontal differences in population density across the lake led to admixture of a denser population into the middle where the samples were taken. This possibility will be discussed in a subsequent section.

By about August 8, first instar animals had become very scarce but subsequent collections showed an increasing number of small animals presumably derived from the release of the animals previously observed as nonephippial embryos. The persistence of the first size group after August 15 can be attributed to the new brood.

The cause of death in the population decreases has not been ascertained. Corpses, recognized by the common-sense principles elaborated by Kastalskaja-Karsinkina (1935), are present in a good many of the early samples, but there were no great increases in the number of corpses just be-

fore or after a population decline. Evidently they fell to the bottom rather quickly, and in a shallow lake the chances of catching corpses in plankton samples are rather small. Daphnia are subject to a number of fungal, bacterial and protozoan diseases, but the preserved corpses that were seen gave no evidence of the cause of their death. The evidence available at present does not suggest that starvation was the cause of death, although more data will become available when Dr. G. W. Prescott's investigation of algae is completed (Prescott *in litt.*).

The distinct mode at the third 5-unit group on August 20 (Fig. 3) gives the impression that the animals from non-ephippial eggs are larger than those from ephippial eggs, but close examination shows that this mode does not represent the smallest animals from non-ephippial eggs, and there is actually little difference. The smallest animals from ephippial eggs fell into the upper part of the first 5-unit group, while those from non-ephippial eggs tended to fall into the lower part of the second group.

The smallest members of the new brood developed from non-ephippial embryos are small enough to fit into the size range of the first instar developed from ephippial eggs. It appears that the instars of the new brood are rather more variable in size than the ephippial brood, for the animals increase in length without producing major modes in the length frequency distribution (Fig. 3). Nevertheless, there is a certain amount of grouping which is reasonably well fitted by the previously determined limits for the animals hatching from ephipipal eggs. In early September, the largest members of the growing brood began to achieve fifth-instar size and presumably to produce ephippia.

It should be noted that most of the small number of non-ephippial animals in the samples after the first week of September appeared to have produced ephippia previously as judged by the profile of the dorsum and the spination of the ventral edges of the carapace (cf. Olofsson 1918). A study of the data (Figs. 3 and 5), suggests that the contribution to the population of animals produced from non-ephippial eggs was relatively unimportant. The number in the new brood is small compared to the number of exephippial animals.

To this point, an attempt has been made to interpret the changes in population size on the assumption that the changes were biologically real, not resulting from sampling error. The two maxima on September 14 and especially 21 are puzzling because there appears to be no preparation for them by production of early instars. The sampler was evidenly working properly, the duplicates agreed well, and the samples and number of animals counted were large, so it is necessary to explain the population changes on a basis other than that of the ordinary sort of statistical sampling error having to do with random distribution. The observation could be explained by assuming that the character of the population available to the sampler was changing. It is perhaps significant that both the population peaks mentioned were accompanied by periods of high wind (Fig. 1). Several possible explanations will be discussed. One possibility is that the vertical distribution involves having most of the animals so near the bottom that the sampler cannot get them except when they have been brought up by the wind. The collections of 1951 show that Daphnia was somewhat more abundant at 2 meters than at the surface, but it is very doubtful that the animals would congregate so densely in the thin layer not sampled that stirring them into the lake would result in the large change observed. Confirmation comes from certain samples in 1952 which contained silt, the sampler obviously having been towed quite close to the bottom. Such samples would be expected to have a consistently much higher population than others, if vertical stratification could account for the observations, but in fact they did not contain unusual numbers. This hypothesis seems further unlikely in view of the coherence of the changes in population age structure.

Although the observed results cannot be explained on the basis of strong vertical stratification, another explanation that comes to mind is the possibility of lateral stratification, for some species of Daphnia have been observed to form aggregates near shore in quiet ponds. If strong inhomogeneities existed in lateral distribution, both the total population changes and some of the changes in proportions of different instars could be produced by movements of water masses in the lake. For this effect to have explained the results, it would be necessary that very dense populations must have built up in the shallow water near shore that was not sampled with the Clarke-Bumpus sampler, and these have been brought suddenly out into the lake by September 21. It seems very doubtful to the author that the required degree of lateral dispersion to shore could have been consistently maintained by Daphnia in the presence of the strong winds that blew (Fig. 1). At no time during the summer did the maximum daily wind velocity for the fastest mile drop below 7 m.p.h., and it was usually more than 10. The minimum daily average was 4.7 m.p.h., but

it was usually considerably more than that. There was no general relation between wind velocity and population. The most that can be said is that the two peaks of population in question followed relative calm, and coincided with strong wind, but that this sequence was not observed earlier. To explain the rapidity and magnitude of the increase, it would probably be necessary that a mass of inshore water containing a local concentration had been bodily transported to the sampling area without much dilution. The observations of Johansen (1911) suggest that great inshore concentrations are not to be expected. It must be pointed out that there are certain relations between changes of wind and population; the three sharp drops in population through early August coincide with changes in wind direction, and some similar changes occurred later.

Ragotzki and Bryson (1953) have shown that in Lake Mendota Daphnia can be locally greatly concentrated and thinned out by currents which produce areas of convergence and divergence. This phenomenon probably is not limited to large lakes, but rather would be governed more by complexity of shape and hydrography. Whether such a pronounced effect would be set up in a lake of the simple shape of Imikpuk under the conditions of wind that existed seems doubtful, but it is possible that a degree of lateral inhomogeneity could develop. Critical data on this point are not available. Qualitative observation of swarms near shore by wading observers are not to be regarded as critical evidence.

An hypothesis that seems to the author to be quite possible on biological grounds is as follows. Great numbers of ephippia were produced in late August and early September. Likely many of them blew to the downwind shore and hatched. The immediate hatching of ephippial eggs of *Daphnia longispina* under proper environmental conditions is reported by Wood and Banta (1937). The result would be a relatively dense population of young animals right at the edge which would not have been sampled. By the time they were stirred out into the lake by the strong winds of September 13 and 14, they had passed through the first five instars, and were sampled as sixth-instar animals. This idea receives some support from evidence based on examination of the non-ephippial animals in samples of September 21 as compared with those of September 10. Olofsson (1918) has shown how to distinguish between non-ephippial animals that have not produced an ephippium and those that have just cast one. The samples of September 21 contained relatively more of the former type than the earlier sample, although the fraction was small in both, and the difference is not statistically impressive. Also, the increase in numbers of loose ephippia in August and September coincided with windy periods.

The smaller peak of September 14 is somewhat different in that it was associated with a transitory peak of Limnocalanus, represented at that time only by adults (Comita 1953). This particular situation possibly resulted from large-scale wind-generated irregularity of distribution in the form of bands parallel to the wind, as described by Stommel (1949), although effort was made to avoid trouble from that source by sampling in duplicate. The fact that periods of strong wind in early August were not followed by abrupt changes in the population suggests that this is in fact a condition which developed only during the end of the summer.

This hypothesis of course could now be exactly tested only by revisiting Imikpuk, a prospect that is not immediately in sight. However, every component of the hypothesis is based on known facts. The difference between the two explanations is that one suggests that the total population of the lake increased at the end of the season, while the other maintains that the changes represent merely local change of concentration in the middle part of the lake brought about by shifts of an inhomogeneously distributed population.

Number of Preadult Instars

The smallest animal observed to carry eggs on August 1 was large enough to belong to the sixth instar. Because of the fact that eggs fall from the brood chambers in preserved samples, it is not certain that smaller animals do not lay eggs. However, animals with enlarged ovaries on July 31 were of fifth instar size, and the presumption is fairly sound that there were five preadult instars, the fifth being juvenile. Work by Anderson (1932) showed that *D. magna* has 5 or more preadult instars, depending on conditions, although Wood, Ingle and Banta (1939) always found 4 in *D. longispina*. It might have been expected that this Arctic form would have evolved a faster rate of development, but such seems not to be the case.

Growth Rate

The progressive increase in mean size of the population (Fig. 4A) is in part a measure of growth rate, but is distorted by the continued addition of small animals by hatching and the sporadic death of large animals. The latter prevents use of the largest animal in each collection to measure the growth rate. Nevertheless, it is possible to give the growth rate in terms of size of instars (Fig. 6). The mean size of animals

of each instar is plotted against instar number, and compared with Daphnia growing in relatively constant laboratory conditions. It is seen that *D. pulex* var. *tenebrosa* in Imikpuk is similar to *D. magna* in the laboratory. The curve is shaped most like that for semi-starved *D. longispina,* although the mean sizes are considerably greater.

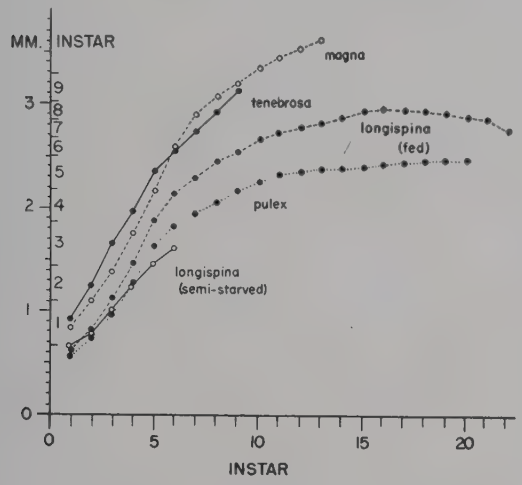


FIG. 6. Growth of *Daphnia pulex* var. *tenebrosa* compared with that of other Daphnia. The length is plotted against instar number. The curve for var. *tenebrosa* shows the mean length of the nine size groups believed to be instars. The range of the size groups is shown on the right-hand scale. The other curves show mean sizes taken from published data. *D. pulex* de Geer (no further taxonomic specification), Anderson, Lumer and Zupancic (1937, Table I). *D. magna* Straus, Anderson (1932, Fig. 4). *D. longispina* (O. F. Müller) fed large quantities of food (fed) and limited quantities (semi-starved), Wood, Ingle and Banta (1939, Tables 24 and 25).

Recognition of Animals Hatched From Non-ephippial Eggs; Length of Spine

As pointed out in connection with the instar analysis, it is difficult to know on the basis of length-frequency distributions alone whether the smallest animals observed in the middle of August represent the new brood of young just hatched from non-ephippial embryos, or whether they have grown from the smaller exephippial animals observed earlier, starting about August 10 or 11.

It had been hoped that some definite criterion would be found which would permit certain recognition of animals of the same size which had been hatched from ephippial and non-ephippial eggs. Poulsen (1940 a and b) studied a population of *D. pulex* in which the exephippial animals were lighter in color and had much shorter spines. In the Imikpuk population the color difference was not found, but there did seem to be a difference in the relative length of the spine.

In this connection a curious observation on the eye pigment is worth describing. All the exephippial animals in the early July collections had a very light-colored eye, the pigment appearing rather reddish brown, as it is in embryos. On July 28 the eyes were slightly darker, on July 31 still darker, and by August 8 all were quite normally dark. At first it was supposed that light eye color characterized exephippial animals, for the non-ephippial embryos developed dark eyes well before birth. However, the darkening seemed to affect animals of all sizes equally, and is therefore very unlikely to have anything to do with the origin of the animals. No explanation is offered, although change in food supply and temperature are possibilities. No changes in technique of preservation were recorded.

Measurements of specimens were made in a number of samples taken on different dates distributed through the season, chosen with particular reference to the period when the non-ephippial eggs were beginning to hatch, in the hope that it would be possible to see if there were still ephippia hatching at that time.

The results (Fig. 7) show that in Imikpuk the exephippial animals have spines that are absolutely and relatively shorter than those hatched from nonephippial eggs, although there is considerable variation in the spine length within any length-class. Early in the season (July 31) the ephippia gave rise to animals with spines ranging from 0.24 to 0.40 mm, or about 25 to 50% of the length. The absolute length of the spine increases little or not at all as the body grows, so that in most of the larger animals the spine is less than 30% of the total length. In strong contrast is the situation on September 2, when the smallest non-ephippial animals, somewhat larger than the smallest on July 31, had spines ranging from 0.68 to 1.02 mm, or about 50% to as much as 80% of the length. It appears that in the animals from non-ephippial eggs the spine shortens at each moult during early life until it reaches about the same length as that of older exephippial animals.

Evidently, populations of the two types of young can easily be separated on the basis of spine length, but there may be difficulty with some individuals. A small animal with a spine 50% of its length cannot be clearly assigned to one or the other group on the basis of its spine length.

The earliest date on which an animal hatched from a non-ephippial embryo certainly occurred seems to be 13 August, although the smallest animal on August 10 could have been, as far as the

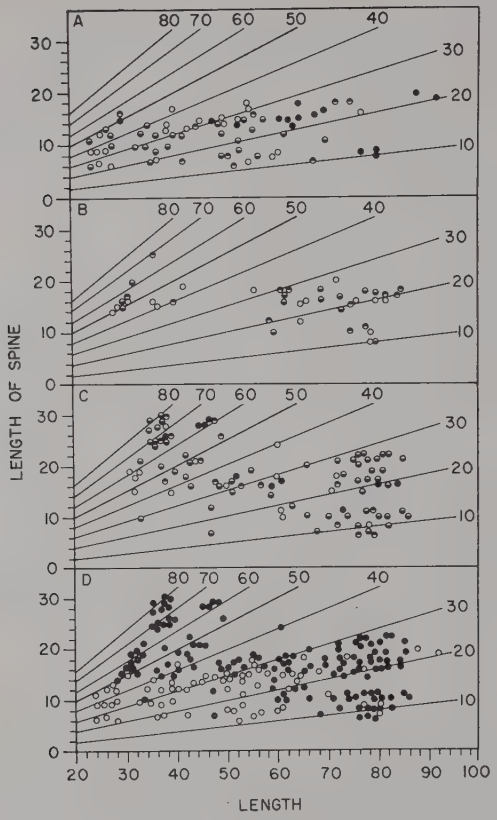


FIG. 7. Relationship between length of Daphnia and length of spine. In each panel the length of an individual and of its spine is represented by a point. The oblique lines show the ratio of the length of spine to length of animal expressed as percentage. In each of the top three panels, data from three or four dates are plotted together. In the bottom panel, the data above are collected together. In each panel the earliest date is shown by an open circle, the next three are shown in order by circle filled in bottom half, circle filled in top half, and circle filled completely. Lengths are given as micrometer units where 1 unit = 0.034 mm. Panel A. 22 and 31 July, 8 and 10 August. Panel B. 11, 13 and 15 August. Panel C. 26 August, 2, 10 and 17 September. Panel D. Open circles, the data of Panel A. Closed circles the data of Panels B and C.

evidence goes, for the spine was very close to 50% of the length.

Duration of Embryonic Period

The time between the peak populations of early and late embryos is seven days, which serves as a minimal estimate of the length of the period of development. It is minimal because presumably the measure gives the time from the middle of the early period to the middle of the late period, without allowing for the time it takes for a new laid egg to develop to middle early stage condition and the corresponding time for the middle late stages to hatch. Another basis for estimation would be the time between the first appearance of eggs in the brood pouch and the first appearance of animals hatched from non-ephippial eggs. The first date can be considered as August 1. The second date is more difficult to place because of the continued presence of small animals hatched from ephippia. The latest possible date is August 13, making the developmental period 12 days, but this is probably an over-estimate because by August 15 enough small ones had appeared to make a distinct group in the length-frequency distribution, and the first ones out must have made their appearance some days earlier. As decided in the previous section, the smallest animal present on August 10 possibly represents a hatch from a non-ephippial egg. On this basis, the period would be 10 days, but this is an underestimate because it represents the fastest developing animal. The average time of development may therefore be estimated as between 10 and 12 days. The temperature of the water during the period of development rose from 7° to 10.5° C. The duration of development of *D. magna* has been reported as considerably shorter at much higher temperatures, varying up to about 72 hours at 25° (Anderson and Jenkins 1942), although Obreschkove and Fraser (1940) got 46 hours at the same temperature for *in vitro* development.

The duration of development is very close to the time between moults, since a batch of eggs is laid just after moulting. Presumably Instar 6 in Imikpuk lasted between 10 and 12 days.

Length-Weight Relationship

In order to determine the mass of the Daphnia population, groups of 25 or 50 individuals were taken from the samples, rinsed in distilled water, laid on weighed coverglasses, and drained of the water. After drying in a desiccator overnight, the coverglasses with the animals were heated on an open hot plate for 1 hour at 60°, cooled in a desiccator, and weighed immediately. This relatively low temperature was used to avoid volatilization of the fat. Each animal was measured before being placed on the coverglass, and the mean length of each group determined. The weights of non-ephippial animals were determined for nine dates and of ephippial animals, without eggs, for three. In addition, 100 early embryos, 100 late embryos, and 100 loose ephippial eggs were weighed.

The data were plotted arithmetically, semi-

logarithmically and double logarithmically in order to ascertain the nature of the relationship. Simple inspection showed that the plot of log weight against length gave a relationship much more nearly linear than either of the others (Fig. 8). The equation of best fit by the least squares criterion is $\log_{10}W = 0.744\ L + 0.076$ where W is dry weight (formalin-preserved) in micrograms, L is length in millimeters. Ephippial animals tend to weigh a little more than those without ephippia, all without eggs. This is in contrast to Berg's results with *D. pulex, D. magna* and *D. cucullata* (1936). The data on embryos are plotted on the same graph, although they cannot be expected to fall onto the line fitted to the post-natal stages. There is a distinct loss in weight as the embryos develop.

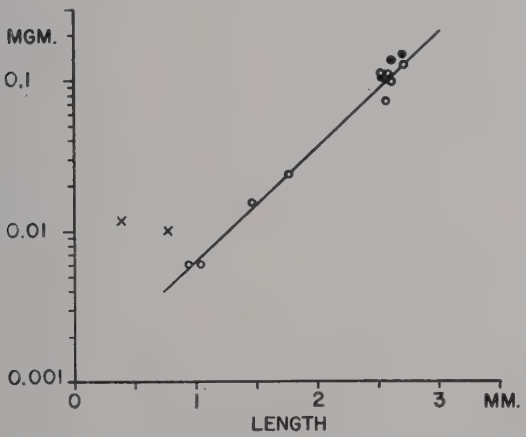


FIG. 8. Length-weight relationship for preserved Daphnia. The crosses represent early and late embryos. Open circles show non-ephippial animals, closed circles ephippial animals, both without eggs. Weight is given on a logarithmic scale.

Since the animals were taken at random from samples, and were not highly selected for uniformity of size before being weighed, the equation must be regarded as an approximation to the true length-weight relationship. The standard deviation for the groups averaged about 0.2 mm.

The material had been fixed in approximately 4% formaldehyde, and stored for more than a year before making the determinations. The effect of formalin fixation on the dry weight of a number of freshwater invertebrates, not including Daphnia, has been studied by Borutzky (1935). If his results can be extrapolated to Daphnia, it would appear that the effect of formalin fixation on the dry weight under the conditions used would not amount to more than the scatter about the regression line shown in Figure 8, although the effect is likely to be systematic.

Mass of Population

The total mass of the population and some of its components were calculated on the basis of the measurements presented (Fig. 4). During July the quantities were quite small, less than 18 mgm./m^3. The increase in the last sample is greatly emphasized as compared with the numbers of animals, since the animals were quite large at that time. The developmental stages, although numerous, formed a very small fraction of the total mass.

CONDITIONS IN 1951

Collections were made on 11 days during the period July 28-September 18, 1951. Since the samples were smaller than in 1952, and were taken with a Kemmerer water sampler which can probably be seen and partly avoided by *Daphnia* (Ricker 1938), the census cannot be as reliable as that of 1952. As far as the data show, the essential features seem to be the same, except that non-ephippial eggs were even less important than in 1952, being almost completely absent. The first ephippial animals were taken on the second date of collection, August 9. The maximum population of 2600 per cubic meter was achieved on August 18; however, during most of the season the recorded population densities were considerably less than those in 1952. There did seem to be a tendency for the population to increase somewhat between September 6 and 15, but the increase is not significant.

The size of every individual collected in 1951 was measured, the largest number on any one day being 79, the smallest 1. During most of the season, both the non-ephippial and ephippial animals were distinctly and consistently smaller than those collected at corresponding times in 1952 (Fig. 4A), even allowing for the fact that the 1951 averages shown on the graph include the new brood of non-ephippial animals. The one exception is that the solitary animal collected on 28 July, 1951, was almost fully grown and contained a middle-stage embryo in the brood chamber. Presumably it represents an unusually early hatch from an ephippial egg. The non-ephippial animals tended to be smaller in 1951 also, except on two dates when the means had to be calculated from very few animals.

Environmental conditions were rather different in the two years, for the lake warmed up much earlier in 1951 to a maximum of 12.5° on August 9. Food supply was probably lower in 1952, since the concentration of phytoplankton chlorophyll was consistently less in the later year by a factor of about 3. This fact discourages interpretation of the difference in Daphnia size as a matter of

food supply; however, the smaller phytoplankton population in 1952 can likely be attributed to grazing by the larger population of Daphnia. It is, of course, possible that 12.5° is supraoptimal, but that remains for determination in the laboratory.

Discussion

The general natural history and population ecology of Daphnia, and the results of laboratory work, are well summarized in papers by Wesenberg-Lund (1926), Brown (1929), Berg (1931), Mortimer (1936), Banta and his collaborators (1939), and Slobodkin (1954). It is unnecessary to summarize here these extended discussions, but it will be useful to mention features of Arctic populations to which the present contribution is pertinent.

In the familiar Daphnia populations of temperate regions, the effective reproduction is brought about by non-ephippial eggs, and population size during the reproductive season is largely regulated by factors operating with the parthenogenetic females. That is, it is conceivable, and even probable, that large differences in the number of surviving and hatching ephippia may usually make relatively little difference in the maximum size of population and production of ephippia achieved during the summer. An unusually low hatch will merely prolong the time required to build the population up to the maximum that can be produced. Ephippial eggs function more as devices for carrying the population through adverse conditions than for multiplying the population.

In Imikpuk, conditions are in strong contrast, if 1951 and 1952 are representative. It appears that the non-ephippial reproduction is of little consequence in maintaining the population, the ephippial eggs serving both to multiply the population and maintain the species through winter. Thus there is only one effective generation each year, with one or possibly two subsidiary generations. The first subsidiary generation is that of non-ephippial eggs which produce a few animals that grow up and presumably produce ephippia very late in the year. The possible second subsidiary generation comes from the presumed immediate hatching of some ephippia at the end of the summer in which they are produced. These animals produce ephippia, not non-ephippial eggs.

Thus, in Imikpuk, the size of the population in any year will depend primarily upon the production and survival of ephippia in previous years. Presumably dried ephippia can survive more than one year, and it is probable that the ephippia hatching in any one year consist primarily of those produced the year before, with some produced in previous years. Failure of the brood in one year would not necessarily result in eradication of the species, but it can be expected that the size of the population achieved will differ greatly in different years.

The production of ephippial eggs is therefore seen to be of primary importance in determining population size in the subsequent year. Each ephippium contains only two eggs. An individual can make more than one ephippium, but in Imikpuk the number is bound to be small because of the time available. One of the living animals which arrived in Seattle carrying ephippia, presumably the first, cast the ephippium, produced another in about two weeks, and carried it until death about a month later. It seems unlikely that in Imikpuk the animals can produce more than three or four ephippia as a maximum. Obviously, there must generally be a very high survival and hatching of the ephippia, or there must be in some years an unusually successful non-ephippial brood to replenish the population of ephippia-producers. In either case, survival of the species must be critically dependent on success of ephippia, and subject to control by the factors which affect the ephippia, particularly at the time the lake melts.

The present data give the impression that as effective ephippial reproduction has evolved in this species, the function of producing non-ephippial eggs has become almost vestigial. The same appears to be true of the populations studied by Olofsson (1918) and Poulsen (1940), although conditions were less severe, and there was more time for production of ephippia than in Imikpuk.

The production of ephippia may now be considered further. In the populations collected by Sars, ephippial females but no males occurred. Sars also found typical *D. pulex* with males which he figured. Juday (1920) mentioned the presence of male *Daphnia pulex* in the North American Arctic, but gave no information about them. Olofsson (1918) described extensive material from Spitzbergen, identified as *D. pulex*, in which no males ever appeared although ephippia were produced. Olofsson's data rather convincingly showed that the organisms must be capable of producing ephippial eggs without the presence of males, and that these eggs must be fertile. His figures also suggest that he was probably dealing with *D. pulex* var. *tenebrosa*.

The papers published together in 1926 by Banta and by Schrader show definitely that a clone of *D. pulex* ("line 1136") was able to produce viable ephippial eggs without fertilization, and for these Banta proposed the name "pseudosexual." Males were never produced. Schrader's cytological

work showed that there was no chromosomal reduction in the production of "pseudosexual" (ephippial) eggs, the diploid number of 24 being retained. Schrader suggested that the unusually large number of chromosomes actually indicates hexaploidy, since five other genera and a different clone of *D. pulex* had 8 as the diploid number. Nevertheless, Mortimer (1936) found 24 chromosomes in *D. pulex* collected near Berlin, and expressed skepticism of the smaller counts published by others. Banta commented that his animals looked much like the figures of the Spitzbergen population published by Olofsson, and himself gives figures that in part document the comparison, but not in sufficient detail to make a certain case for the identity. The fornices were not figured, and nothing was said about the characteristic dorsal darkening to which the varietal name owes its origin. Banta's clone would produce ephippia but not males when crowded, but otherwise would reproduce by ordinary parthenogenetic eggs. Moreover, an individual could alternate in producing the two types of egg in any order.

The most extended study of any Arctic population reported appears to be that of Poulsen (1940 a and b), who had fortnightly collections from Langsø in East Greenland for an entire year, and less regular collections from other waters. His population of *D. pulex* likewise never produced males, although many ephippial animals appeared. The situation was very much like that in Imikpuk in that there was a period of production of non-ephipipal eggs in the middle of the summer, and a later production of ephipipal eggs exclusively, without male. The activity of the population took place during a longer time than in Imikpuk. The ephippial animals continued to inhabit the lake until April, after which the population was represented only by ephippia for two months. In June, the ephippia began to hatch, giving rise to the new generation that produced non-ephippial eggs. The population probably persisted much longer under the ice in Langsø, but the lack of net collections in Imikpuk after December does not permit the exact date of dying out of the population of active animals to be set.

The taxonomic status of Poulsen's *Daphnia pulex* is not clear, although his figures suggest that he may have had var. *tenebrosa*.

The consistent absence of males in these Arctic populations is very interesting. Clearly the ability to produce fertile resting eggs without males has a survival value to an Arctic species faced with the necessity of producing many offspring in a short time at a low temperature. It occurred to the author that the ability to produce ephippial eggs parthenogenetically would not necessarily imply a loss of the ability to produce males. The results of a great deal of experimental work and observation of natural populations point to the production of males and of ephippial eggs by Cladocera as being responses to the kind of environmental conditions which may precede unsatisfactory or even lethal conditions for maintenance of a population. It is sometimes said that unfavorable environmental conditions lead to male production, but a more accurate description of the facts would be that something about the conditions associated with crowding will initiate amphigonous reproduction. In addition, abrupt changes in temperature may have an effect. The specific factors for male production are somewhat different from those for ephippial egg production. Although intersexes have been described, there appears to be no evidence of functional hermaphrodites.

Now a population density equivalent to about 100,000 animals per cubic meter has often been used in the laboratory to cause abundant male production although males can appear at smaller densities than this in nature. Berg (1931) showed that a form identified as *D. longispina* subsp. *hyalina* which maintained itself in small populations exclusively by parthenogenesis in Vierwaldstättersee, would nevertheless produce males in suitable crowded conditions in the laboratory.

It was therefore of considerable interest to learn from Dr. Brooks after the bulk of this paper was written that he had found males in a population of *D. pulex* var. *tenebrosa* collected by Dr. James Lynch in Eastern Washington. Subsequently Dr. Lynch kindly provided living animals from which a culture was established. Males and ephippia have been produced in cultures at 8° and 15° at a degree of crowding equivalent to approximately 150,000/m^3. The animals were abundantly fed with Fleischmann's dry activated yeast. It is hoped to make further studies of the reproduction of this organism.

It then became of considerable interest to know if the Point Barrow population was capable of producing males. Unfortunately, the live animals sent from Point Barrow arrived in an advanced stage of production of ephippia and it has not yet been possible to rear crowded cultures from the dried ephippia available. However, it seemed worthwhile to attempt to determine if conditions ever exist in the Arctic suitable for male production. A suggestive observation was made by Haberbosch (1920) who found male *D. pulex* in a pool, in only one of many collections in Greenland. While there are no data about pop-

ulation density, and the varietal identity of the animal is not certain, it is very suggestive that Haberbosch was dealing with a Daphnia that apparently produced ephippia without males in other waters. It would be expected that the densest populations would develop in a pool such as that in which he found males.

Therefore, it was in order to examine unusually crowded Arctic populations. The population of Daphnia in Imikpuk was less than 4000/m³ at the maximum, obviously not nearly the density that has been required in species that regularly produce males. The maximum density of Daphnia found in any of the localities sampled by Comita was about 16,000/m³ in Ikroik on 14 August, 1951.

There are reports of small tundra pools swarming with entomostraca, but quantitative data on population density of Daphnia in such locations are scanty. Dr. Mohr had collected material from tundra pools in which he observed small crustaceans in swarms. He kindly supplied samples from one of these locations near Point Barrow, which contained the species under discussion. Dr. Brooks has examined the material and stated that the smallest individuals are either very young, immature males or are nearly male intersexes. Unfortunately, material was not collected from that location at a later date and it is not possible, therefore, to make a statement about the later development of these animals. It is quite evident that *Daphnia pulex* var. *tenebrosa* in the Point Barrow region is capable of a male-producing response to crowded conditions. Data do not exist on the actual population density at the time Dr. Mohr's collection was made, but it is hoped to secure more material collected from crowded populations in the Point Barrow region and to measure the population density.

It is noteworthy that Banta's thelyotokous clone of *D. pulex* never produced males, even under conditions in which other clones would (1939, p. 258). It may well be that some clones of the species have lost the male-producing reaction, but it might have been expected that this would have happened in the Arctic, not at latitude 42°N where Banta got his clone. Obviously many interesting questions await study, and the solutions will come from a combination of widespread observation coordinated with a well-conceived laboratory analysis.

Summary

1. *Daphnia pulex* var. *tenebrosa* Sars 1907 was a prominent member of the zooplankton of Imikpuk, a shallow lake near Point Barrow, Alaska, sampled quantitatively in 1951 and 1952. It is an abundant and widespread arctic species, but is occasionally found at lower latitudes.

2. Changes in the density and the size composition of the population are described (Fig. 1). Adults died out during the winter, and the population overwintered as ephippial eggs. Animals hatched from ephippial eggs just as the ice was melting around the edge of the lake early in July, 1952, and in the course of three weeks grew to maturity. Apparently sporadic mortality caused decreases in the population, which was replenished by continued hatching of ephippia. One brood of non-ephippial eggs was produced which gave rise to a small generation that apparently produced ephippial eggs in September. Their development was followed in detail (Figs. 1 and 2). None of these animals produced non-ephippial eggs. This generation formed only a small part of the total population.

3. Most of the exephippial animals produced ephippial eggs as their first brood. The possibility exists that some of the ephippia produced in 1952 hatched before the lake froze in September, making an increase in population. Thus there is one principal generation each year with exephippial animals producing ephippia. There is a subsidiary generation of non-ephippial eggs by some of the exephippial animals. Further, possible hatching of ephippia during the year in which they were produced makes a second subsidiary generation. Ephippial eggs are more important than non-ephippial eggs in reproducing the species. The population size achieved in any year is highly dependent on the factors affecting survival and hatching of ephippia.

4. The duration of the embryonic period of the non-ephippial eggs was between 10 and 12 days. The water temperature varied from 7.0° to 10.5° during development.

5. An analysis of the probable instar composition of the population was made on the basis of length-frequency data (Fig. 3), and the growth rate determined (Figs. 4 and 6).

6. The length-weight relation was determined (Fig. 8), and from it the mass of the population computed (Fig. 4).

7. No males occurred. The ephippial eggs evidently do not require fertilization.

8. A discussion is given of some of the published work on Arctic Daphnia populations and related laboratory work.

References

Anderson, B. G. 1932. The number of preadult instars, growth, relative growth and variation in Daphnia magna. Biol. Bull., **63**: 81-98.

———, **and J. C. Jenkins.** 1942. A time study of events in the life span of Daphnia magna. Biol. Bull., **83**: 260-272.

———, **H. Lumer and L. J. Zupancic.** 1937. Growth and variability in Daphnia pulex. Biol. Bull., **73**: 444-463.

Banta, A. M. 1926. A thelytokous race of Cladocera in which pseudosexual reproduction occurs. Zeit. Indukt. Abstamm-und Vererb., **40**: 28-41.

Banta, A. M. et al. 1939. Studies on the physiology, genetics and evolution of some Cladocera. Carnegie Inst. Wash. Paper **39**: 1-285.

Banta, A. M., and T. R. Wood. 1939. Genetical studies in sexual reproduction. (*In* Banta *et al.*, 1939, pp. 131-181.)

Berg, K. 1931. Studies on the genus Daphnia O. F. Müller, with especial reference to the mode of reproduction. Dansk Naturhist. Forening., Vidensk. Medd., **92**: 1-222.

———. 1936. Reproduction and depression in the Cladocera, illustrated by the weight of the animals. Arch. Hydrobiol., **30**: 438-460.

Borutzky, E. B. 1935. Zur Fragen über die Technik der quantitativen Untersuchungen der Bodenfauna. IV. Die Methode der Bestimmung der Trockengewichts der fixierten Materials. Trudy Limnol. Sta. Kossino, **19**: 1-19.

Brooks, J. L. 1946. Cyclomorphosis in Daphnia. I. An analysis of *D. retrocurva* and *D. galeata*. Ecol. Monogr., **16**: 409-447.

Brown, L. A. 1929. The natural history of cladocerans in relation to temperature. Amer. Nat., vol. 63; I. Distribution and the temperature limits for vital activities. Pp. 248-264; II. Temperature coefficients for development. Pp. 346-352; III. Preadaptation and dispersal. Pp. 443-454.

Clarke, G. L., and D. F. Bumpus. 1950. The plankton sampler—an instrument for quantitative plankton investigations. Amer. Soc. Limnol. and Oceanogr., Sp. Pub. No. 5: 1-8 (2nd ed.).

Comita, G. W. 1953. A limnological study of planktonic copepod populations. Ph.D. Thesis, University of Washington. 196 pp.

Comita, G. W., and W. T. Edmondson. 1953. Some aspects of the limnology of an arctic lake. Stanford Univ. Pub. Univ. Ser. Biol. Sci., **11**: 7-13.

Haberbosch, P. 1920. Die Süsswasser-Entomostracen Grönlands; eine faunistische, oecologische und tiergeographische Studie. Zeits. f. Hydrol., **1**: 136-184, 245-349.

Johansen, F. 1911. Freshwater life in north-east Greenland. Medd. om Grønland, **45**: 321-337.

Juday, C. 1920. Cladocera. Rep. Canadian Arctic Exp. 1913-18, **7** (H): 1-8.

Kastalskaja-Karsinkina, M. A. 1935. Methode zur Bestimmung der lebenden und abgestorbenen Planktonkomponenten an fixiertem Material. Arb. Limnol. Stat. Kossino, **19**: 91-107 (Russian, with German summary).

Langford, R. R. 1953. Methods of plankton collection and a description of a new sampler. Jour. Fish. Res. Board Canada, **10**: 238-252.

Mortimer, C. H. 1936. Experimentelle und cytologische Untersuchungen über die Generationswechsel der Cladoceren. Zool. Jahrb., Abt. f allg. Zool., **56**: 323-388.

Obreshkove, B., and A. W. Fraser. 1940. Growth and differentiation of Daphnia magna eggs in vitro. Biol. Bull., **78**: 428-436.

Olofsson, O. 1918. Studien über die Süsswasserfauna Spitzbergens. Zool. Bidr. från Uppsala, **6**: 183-646.

Poulsen, E. M. 1940a. The zoology of East Greenland. Freshwater Entomostraca. Medd. om Grønland, **121**: 1-73.

———. 1940b. Biological remarks on Lepidurus arcticus Pallas, Daphnia pulex de Geer and Chydorus sphaericus O. F. M. in East Greenland. Medd. om Grønland, **131** (1): 1-50.

Prescott, G. W. 1953. Preliminary notes on the ecology of freshwater algae in the arctic slope, Alaska, with descriptions of some new species. Amer. Midl. Nat., **50**: 463-473.

Ragotskie, R. A., and R. A. Bryson. 1953. Correlation of currents with the distribution of adult Daphnia in Lake Mendota. Jour. Mar. Res., **12**: 157-172.

Ricker, W. E. 1937. Statistical treatment of sampling processes useful in enumeration of plankton organisms. Arch. Hydrobiol., **31**: 68-84.

———. 1938. On adequate quantitative sampling of the pelagic net plankton of a lake. Jour. Fish. Res. Bd. Canada, **4**: 19-32.

Rugh, R. 1948. Experimental embryology (Revised). Minneapolis: Burgess, 480 pp.

Sars, G. O. 1898. The Cladocera, Copepoda and Ostracoda of the Jana Expedition. Ann. Mus. Zool., Acad. Imp. Sci., St. Petersburg, **3**: 324-359.

Schrader, F. 1926. The cytology of pseudo-sexual eggs in a species of Daphnia. Zeit. Induk. Abstamm.- und Vererb., **40**: 1-27.

Slobodkin, L. B. 1954. Population dynamics in *Daphnia obtusa* Kurz. Ecol. Monogr., **24**: 68-88.

Stommel, H. 1949. Trajectories of small bodies sinking slowly through convection cells. Jour. Marine Res., **9**: 24-29.

Suomalainen, E. 1950. Parthenogenesis in animals. Adv. in Genetics, **3**: 193-253.

Vollmer, C. 1912. Zur Entwicklungen der Cladoceren aus dem Dauerei. Zeit. Wiss. Zool., **102**: 646-700.

Wesenberg-Lund, C. 1926. Contributions to the biology and morphology of the genus Daphnia. Mem. Acad. Roy. Sci. Lett. Danemark, Sect. Sci., (8) **11**: 89-250.

Wood, T. R. and A. M. Banta. 1937. Hatchability of Daphnia and Moina sexual eggs without drying. Int. Rev. ges. Hydrobiol. Hydrogr., **35**: 229-242.

Wood, R. R., L. Ingle and A. M. Banta. 1939. Growth and reproductive characteristics of *Daphnia longispina*. (*In* Banta *et al.*, 1939, pp. 182-200.)

XYLEM LAYERS OF TREES AS RELATED TO WEATHER AND ALTITUDE IN THE NORTHERN ROCKY MOUNTAINS

R. Daubenmire
Department of Botany, The State College of Washington, Pullman, Washington

Studies of the course of diametral changes in coniferous trees at different altitudes in the western foothills of the Bitterroot Mountains have shown: (1) that for the three taxa studied, the time when growth begins is surprisingly similar at high and low elevations, even though temperature conditions differ widely at this season (Daubenmire 1949), (2) that for the 5 taxa studied and seasons tested, growth progresses much more slowly in individuals at high altitude during the first few weeks of the growing season (Daubenmire 1946, 1949), and (3) that, for the four taxa studied, drouth-correlated shrinkage beginning at the end of the growing season in midsummer is pronounced only at low altitude (Daubenmire 1946). Assuming that trees at high and low altitude are genetically undifferentiated,[1] the last two points above suggest that low temperature may retard growth early in the growing season at high altitude, whereas drouth may interfere late in the season at low altitude. A test of this hypothesis was the purpose of the present study. The fact that others (Büsgen and Münch 1929, Laitakari 1920, Flury 1927, Primault 1953) have found temperature to be more critical at high latitudes and altitudes but precipitation more critical in warm latitudes and at low altitudes suggested that homologous relations might characterize growth at high and low altitudes here in the Rocky Mountains. Even studies of trees in different microclimates have suggested the same hypothesis. Thus, on a north-facing slope in New Jersey, Cantlon (1953) found that diameter increment in *Quercus* was retarded in spring, when compared with trees on a south-facing slope, whereas the relationship was reversed later as the environmental water balance became less favorable.

The essential concomitance of the seasons of diameter growth of the coniferous trees, and their confinement to approximately the three months, May, June, and July, facilitate a comparative study of current weather as related to the thickness of the growth layers in this region. It seemed logical to center attention upon the known growing period, for in this quasi-oceanic climate with heavy winter precipitation, the soils are everywhere at or above field capacity in spring when growth begins, so that the adequacy of preseason precipitation is scarcely a question. Furthermore, winter temperatures are adequate to meet the cold requirements of all these trees even well below their natural altitudinal limits, whereas the winters are not so cold as to produce injury that would suggest that temperature just prior to the growing season commonly affects the amount of growth.

Since at the beginning of the growing season, soil moisture is abundant and showers frequent, variations in temperature at this time should be more critical than variations in precipitation. For this reason, and also because dendometric studies showed slower growth at high altitude in spring, a special attempt has been made to correlate the temperatures of the month of May with total growth. As the season progresses, temperature rises, the rains diminish in effectivity, and the upper soil horizons dry to varying depths (McMinn 1952). In theory at least, moisture should gradually supercede temperature as the factor most likely to condition active growth, and this is in harmony with the strong drouth-induced shrinkage observed at low altitude. Consequently, total growth has been studied especially in relation to July temperature.

Field Methods

Four taxa of trees were studied on the Thatuna Hills (rarely referred to as the Palouse Range), or on adjacent Tomer's Butte, in Latah County, Idaho. These taxa, listed in order of increasing mesophytism as indicated by their relative abilities to extend their distributions down the montane moisture-temperature gradient, are *Pinus ponderosa* Laws., *Pseudotsuga taxifolia* (Poir.) Britt. var. *glauca* (Mayr) Sudw., *Abies grandis* Lindl., and *Thuja plicata* Donn. The altitudinal range of these hills is sufficient that each of these trees reaches its highest and lowest elevational limits with respect to the vegetational zonation, and a group of five trees representing each taxon at its uppermost limits was compared with another group of five trees at the lower biogeographic

[1] All trees referred to in the Moscow region were growing within a circle having a radius of 7 km. and a vertical range of altitude of 540 m. Among wind-pollinated coniferous trees, it seems safe to assure that no significant impediment to gene flow could develop in such limited space.

limit. The groups selected do not represent the absolute highest or lowest individuals with respect to sea level, but were selected only because of their extreme positions in relation to the pronounced zonal sequence of plant associations from the warm dry foothills to the cold and moist mountain summits.

The first five trees encountered in each stand were used, providing (1) the number of growth layers exceeded 50 at a height of 1 m. (most of the trees were less than 70 years old), (2) the trees appeared to be healthy specimens fully as tall as their neighbors, (3) there appeared to have been no recent disturbance of environment caused by fire, logging, grazing, road construction, etc., and (4) providing the trees sampled were scattered sufficiently that the details of natural variations in the intensity of competition which affected one individual could have no appreciable effect upon another used for study. Two opposed radii per tree, taken about 1 m. from the tree base, were used in an effort to reduce the error resulting from unequal deposition of xylem at different points over the cambium, which some workers have found considerable (*e.g.,* Shreve 1924). If weather exerts a dominating influence upon tree growth, this should be revealed by 10 radii from 5 trees selected as described above. The number of trees and radii used here is certainly adequate to compare with the auxinometric studies in which three-tree populations gave consistent results with different taxa and different seasons. Cores were removed with a Swedish increment borer, and after drying, these were glued into grooved boards, sanded smooth, and given a coat of shellac to facilitate measurement.

Treatment of the Data

Weather records made by the U. S. Weather Bureau at Moscow, Idaho, were used. Moscow is situated about 15 km. from the most remote group of trees used for climatic comparison, and lies in the grassland of the basal plain at an altitude of 810 m. whereas the tree stations lie on the mountain slopes between 940 and 1465 m. Thus, the mean monthly precipitation and temperature data for Moscow are not directly comparable with any of the tree habitats, but it seems safe to assume that weather trends are similar throughout, and this is all that is required by the methods of analysis used.

Two statistical methods of showing the degree of relation between weather and xylem increment have been used. One widely used method involves the calculation of correlation coefficients. For 50 pairs of observations, the coefficient must reach a value of 0.27 to indicate a high probability of climatic influence upon tree growth.

Because all trees showed a strong decline in the thickness of xylem layers when plotted against age, whereas the 50-year weather record showed no such trend, the actual measurements of the layers for one population of 10 cores were averaged, then the averages adjusted as follows. A second tilted abcissa was constructed to parallel a straight line drawn through two points, one point representing the average width of layers for the first decade, the other representing the average for the last decade. This abcissa was moved down far enough on the graph to be lower than all the points representing growth. The adjusted values for width were then taken to be the differences between the tilted abcissae and the actual values plotted relative to the normal abcissae. The object of this manipulation was to eliminate, as much as possible, an element of progressive change in thickness of layers resulting from the increasingly larger volume of the woody cylinder over which the annual production of new wood must be spread, and thus make the comparisons between weather and growth more direct.

If it is correct that the application of Pearsonian correlation (which was originally designed for population analysis) to a time sequence may not be valid (Glock 1941), the employment of a second technique as outlined below, is highly desirable as a check upon conclusions suggested by correlation coefficients.

The second method used consists of recording a plus for each year when both tree growth and temperature (or precipitation) increase, in comparison with the previous year, and a minus when the trends are not harmonious (Shreve 1924). If there is no measurable causal relation, a long series of years should yield an equal sum of plus and minus trend signs, but if there is imbalance, the direction and degree of relation is proportionate to the direction and degree of imbalance. It has been assumed that a value of twice the standard error indicated the minimum level of deviation from the balanced ratio of agreements to disagreements that might have possible significance as indicating climatic control over diameter growth. Standard error for a set of observations (49 observations possible out of 50 year's data) was calculated as follows, with A representing agreements and D representing disagreements:

$$\text{S.E.} = \sqrt{\frac{A \times D}{A + D}} = \sqrt{\frac{24.5 \times 24.5}{49}} = 3.5$$

Agreements of 17 or less, or 32 or more, are therefore taken as threshold values suggesting climatic

influence, with 24.5 agreements out of 49 observations taken as indicating a perfect lack of influence.

Results of the Studies Near Moscow

Only two correlation coefficients were obtained that may be considered as possibly significant from a mathematical standpoint (Table I). One of these suggests that along the cool-moist edge of *Pinus* distribution, precipitation in June-plus-July, at least, benefits growth. But this is at odds with the fact that these trees were growing in about as moist an upland evironment as the species may be found. If any trees of this species are really benefitted by summer rains, they should be those situated at the warm-dry limits which form lower timberline, but correlation coefficient are not significant in that comparison.

A second coefficient high enough to merit attention indicates that along the warm-dry edge of *Abies'* range, heat during the growing season is detrimental. The coefficient is even weaker than the one discussed above, and if heat is important, its influence must be direct rather than through the water balance, for an abundance of rain is not beneficial, judged by the same technique.

In Table I, trend analyses also are given for the same comparisons which were tested by the correlation coefficient methods. Referring to the column headed "10 radii," here again only two[2] relationships attain values arbitrarily selected as indicating possible influence of weather on xylem formation. It would appear that, along the cool-wet limits, the growth of *Pseudotsuga* is reduced by increasing heat during the growing season, and that along the warm-dry limits of *Thuja*, summer precipitation is detrimental. Both suggestions are at odds with the fairly well-established facts that heat and dryness are, respectively, becoming more critical, so that the tenability of the mathematical suggestion is seriously jeopardized. It is significant that in neither case does the value much more than exceed the threshold of possible significance, and that neither of these two weakly positive results of trend analysis coincide with the two weakly positive results of the correlation coefficient analysis. In addition, dendrometer studies have shown that different species respond to moisture deficiency in a similar manner (Daubenmire 1946), whereas there is no such correspondence shown in the present analyses. It is clear that the thickness of xylem layers in trees at their upper altitudinal limits is no more augmented by above-average warmth in May than in individuals at the lower altitudinal limits. And, trees at the lower limits are no more benefitted by above-average rainfall in July than are those at the higher limits. The conclusion, therefore, seems warranted that the delayed beginning of stem thickening at high altitude does not represent response to cool conditions to such an extent that the total annual increment is reduced. Nor does the pronounced later-summer shrinkage at low altitude represent dehydration sufficient to curtail cambial activity.

[2] Thus, the criterion tentatively selected to differentiate possible significance from relatively certain insignificance in trend analyses seems to be exactly as rigorous as the standard criteria for correlation coefficients.

Table I. *Correlation coefficients and trend analyses for diameter increment and weather of the growing season, 1900 through 1949. Values of possible significance are indicated by asterices*

Taxon	Series	Weather statistic	Correlation coefficient	Trend agreements 10 radii	Trend agreements 20 radii
Pinus	High	May T	+0.0674	20	26
		May-Jun-Jul T	−0.0421	21	29
		Jul P	+0.1504	19	26
		Jun-Jul P	+0.3310*	25	28
	Low	May T	−0.1053	24	22
		May-Jun-Jul T	−0.2548	21	20
		Jul P	+0.0822	25	25
		Jun-Jul P	+0.2623	31	28
Pseudotsuga	High	May T	+0.1850	18	23
		May-Jun-Jul T	+0.0002	16*	24
		Jul P	+0.0013	21	23
		Jun-Jul P	+0.2580	23	23
	Low	May T	+0.1179	22	19
		May-Jun-Jul T	−0.0665	22	22
		Jul P	+0.1175	21	19
		Jun-Jul P	+0.2370	24	24
Abies	High	May T	+0.0317	27	24
		May-Jun-Jul T	+0.1345	23	23
		Jul P	−0.1280	22	23
		Jun-Jul P	+0.0471	21	25
	Low	May T	−0.2237	26	25
		May-Jun-Jul T	−0.3104*	23	26
		Jul P	+0.1267	27	24
		Jun-Jul P	+0.1483	24	25
Thuja	High	May T	+0.2027	31	29
		May-Jun-Jul T	−0.1042	24	23
		Jul P	−0.0132	18	16*
		Jun-Jul P	+0.1658	25	24
	Low	May T	+0.0135	26	28
		May-Jun-Jul T	−0.2519	23	25
		Jul P	−0.0282	21	19
		Jun-Jul P	+0.1950	17*	17*
Pinus	Spokane	May T	.....	23	..
		May-Jun-Jul T	.....	26	..
		Jul P	.....	23	..
		Jun-Jul P	.....	20	..
Pseudotsuga	Spokane	May T	.....	15*	
		May-Jun-Jul T	.....	18	
		Jul P	.....	19	
		Jun-Jul P	.....	24	..

If, as the above studies indicate, weather during the season of enlargement is not a dominant factor governing variation in wood increment of these species growing in this area, the question next arises as to whether the patent variations from year to year are caused by the external environment or by forces operating within the plant. If any climatic force is controlling, there should be good agreement in the sequences of thick and thin layers among the trees of one stand, and especially between opposed radii of the same tree. But if cambial activity at one point is determined more by internal factors, or at least by factors more localized than weather, opposed radii might not show the same sequence of thick and thin layers. The trend analysis technique appears well-suited to making such a test.

Using the same criteria for levels of possible significance in trend analyses, the results for the Moscow series in Table II show that correlation between opposed radii is barely within the range considered possibly significant, demonstrating a considerable amount of variation in wood layers that cannot be attributed to an external master force such as weather. Using the criterion based upon standard error mentioned earlier, in 16 out of 40 trees agreement does not reach the level required for significance! The degree of sensitiveness to weather is similar among the four taxa, and is similar along both upper and lower limits of the ecologic ranges of the taxa.

The possibility suggested itself that a larger sample might have yielded more definitive results, so a second collection was made in the Moscow region and trend analyses determined from populations thereby augmented to 10 trees, 20 radii. In this test two possibly significant figures were obtained (Table I),—at its upper limits *Thuja* seems adversely affected by increases in July precipitation, and at its lowermost limits an increase in June-plus-July precipitation is detrimental. Only the latter is consistent with the results of the earlier auxinometric study, and neither of the two trend values is very pronounced. Doubling the population, therefore, did not produce a more definitive relationship between xylem increment and current weather.

Studies at Spokane

Most of the trees studied were rooted in heavy soils derived in part from loess that contains volcanic ash. The possibility suggested itself that perhaps the highly favorable water storage capacity of these soils in the mountains near Moscow might play an important part in compensating for the dryness of summer and thus reduce the control by growth by weather. To test this hypothesis, five trees of *Pinus ponderosa* were sampled along the eastern bluff of Hangman (Latah) Creek in Spokane, Washington. This site (*Pinus/Agropyron spicatum* habitat type) was chosen because trees at the top of this bluff are several hundred meters above the stream, they are exposed to the full impact of dry westerly winds blowing across the valley, and they must draw their moisture from sandy glacial till. Also five *Pseudotsuga* trees were sampled a few kilometers to the south of Spokane near the summit of a high gravelly ridge where they are growing at the dry limits of the ecologic range of the taxon on a *Pseudotsuga/Physocarpus malvaceus* habitat type. Measurements of pairs of opposed radii of both these populations were analysed by the trend method, but the correlations were scarcely greater than with the individuals growing on heavy soils (Table I). The sole exception is that heat in May seems possibly detrimental to diameter increment in *Pseudotsuga*.

The course of growth in these last two groups of trees is of sufficient interest to illustrate graphically in Figures 1 and 2. In *Pinus* (Fig. 1), there is considerable discrepancy in the course of growth among the trees, and correlation between opposed radii is so weak that cross-dating would be uncertain if radii originated from different trees. Especially notable is the pair of curves at the top of Figure 1. The results on this habitat are essentially identical to those for *Pinus* in the Moscow region.

Pseudotsuga (Fig. 2), in contrast, shows strong correlation between opposed radii, and the coincidence of peaks in curves for scattered trees suggests the existence of a master factor-complex, presumably climate, which overshadows other causes of variation in width of xylem layers. It is not the purpose of the present paper to determine which environmental variables are most closely associated with this synchronized growth pattern in this particular population, but several conclusions based on the graphed data are relevant to the objective as stated at the beginning of the paper:

(1) As a result of either genetic or environmental difference, certain groups of trees (*e.g.*, the Spokane *Pseudotsuga* population) show climatic control of diameter growth whereas other groups (*e.g.*, the Spokane *Pinus* population and the Moscow *Pseudotsuga* population) do not.

(2) Where climatic influence is evident, a population of 10 radii from 5 trees appears to provide an adequate record of growth fluctuations.

(3) The criterion of significance for the inter-

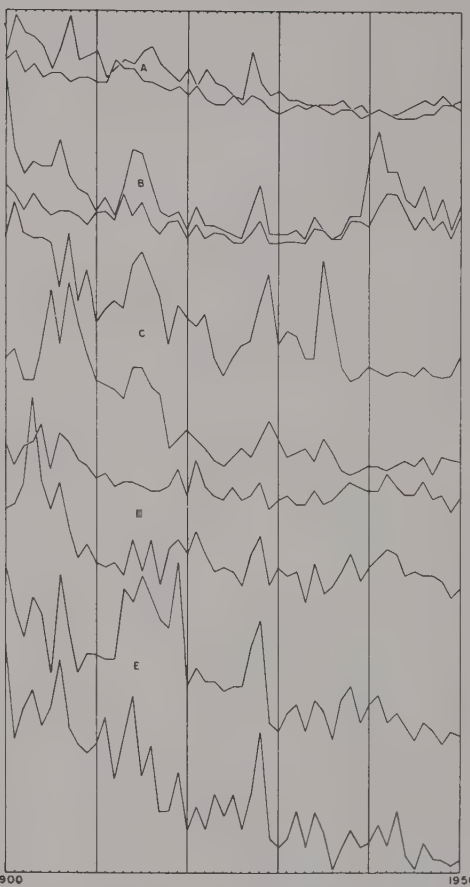


FIG. 1. Relative widths of xylem increments over a 50-year period for five trees of *Pinus ponderosa* growing in the southern edge of Spokane, Washington. The lines above and below each letter represent opposed radii of the same tree.

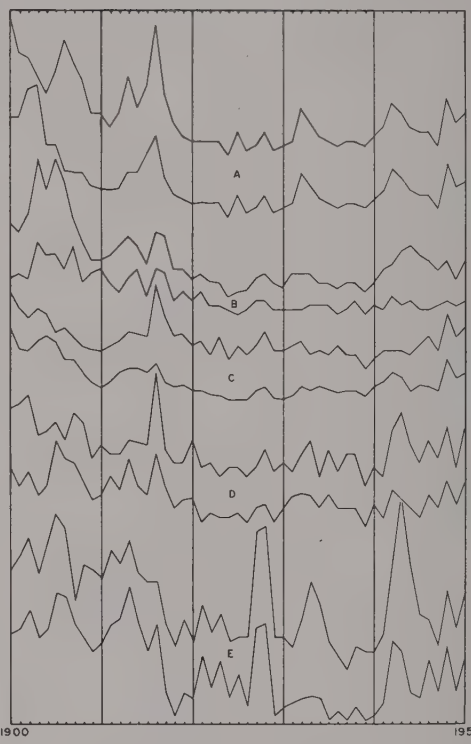


FIG. 2. Relative widths of xylem increments over a 50-year period for five trees of *Pseudotsuga* growing just south of Spokane, Washington. The lines above and below each letter represent opposed radii of the same tree.

pretation of trend agreements which was adopted early seems justified when the results of the two figures and Table II are considered. The curves for *Pinus* at Spokane indicate very small influence of climatic factors in determining growth and the average agreements for the 10 radii of 5 trees is 30 (= 30/49 = 61% agreement) which was assumed to be below the threshold value (32) required for possible significance. The curves for *Pseudotsuga* at Spokane show strong climatic influence and the average agreement is 38 (= 78%), which falls well above the assumed critical value.

(4) Standard temperature and moisture data representing the season of diameter growth for those years when *Pseudotsuga* grew exceptionally well appear unrelated to the relative thickness of the xylem layer. Nine years with conspicuously thick xylem layers have mean May temperatures ranging from 10.9 to 16.4°C., but the total range for all 50 years is almost exactly the same: 10.9

TABLE II. *Comparisons of agreement in trend on opposite sides of the same tree, 1900 through 1949. Values of possible significance are indicated by asterices*

Region	Taxon	Series	Individual trees 1	2	3	4	5	Ave.
Moscow	*Pinus*	High	37*	32*	40*	28	35*	34*
		Low	31	37*	38*	36*	33*	35*
	Pseudotsuga	High	29	37*	37*	31	28	32*
		Low	36*	35*	38*	39*	39*	37*
	Abies	High	37*	28	28	38*	39*	34*
		Low	31	28	31	28	30	30
	Thuja.	High	32*	34*	34*	33*	35*	34*
		Low	31	37*	29	29	28	31
Spokane	*Pinus*	..	35*	31	17	30	35*	30
	Pseudotsuga	..	36*	27	35*	38*	38*	38*

to 16.8. Therefore, the outcome of the trend test, judged empirically as of possible low significance, seems even less likely a true indication of the control of diameter growth by current weather conditions. Further special tests were made in which it was hypothesized that heat in May might be offset by deficient precipitation in July, and vice versa, with a possible cumulative effect of high temperature in May plus high precipitation in July. The results were consistently negative. Both 1906 and 1933 were years of exceptionally good growth, but May temperature and July precipitation were below normal both years.

(5) *Pseudotsuga* appears to be more susceptible to climatic influence in the Spokane area, and the identity of rings is more certain, in comparison to *Pinus ponderosa*. The last point is supported by the fact that 9/10 of the *Pseudotsuga* curves (Fig. 2) show a growth maximum in 1928. Possibly the same growth maximum appears in the nearby stand of *Pinus ponderosa*, but in one tree apparent misidentification of the layers resulted in the maximum falling in "1927," and in another in "1929." Supernumerary and omitted rings have been known for more than half a century, but it is doubtful if this phenomenon is of very great significance in this region. Field studies with a binocular microscope of *Pinus* stumps, on which different radii were worked down to a smooth surface with a half-round chisel, have shown less discrepancy in ring correlation in the Moscow region than is suggested by the Spokane *Pinus* curves.

Different individuals representing the same taxon and growing in the same stand might conceivably differ in their sequences of thick and thin rings as a result of different timing and intensities of damage suffered from wind or snow breakage, insect defoliation, parasite invasions that are finally repelled, from squirrel pruning, from differing time of release from competition by the death of neighboring trees, from mild surface fires that do no more than burn strips across the forest floor or from local soil creep that disturbs roots. Such factors should permit conformity of ring sequences on difference radii of the same tree, even if there was not uniformity from tree to tree.

Not only have incomplete rings with limited vertical or periclinal extent been reported, but unequal growth over the cambial cylinder has been well-established. Glock (1941) cites nine such studies.

Varied responses of different portions of the same cambial cylinder might accrue from limited damage of the types listed above, which affect only one xylem tract. But if conforming ring sequences cannot be traced along xylem tracts, we must assume that the response of different patches of cambial cells to growth-initiating stimuli varies in an unpredictable manner.

Variations in cambial activity within or among trees are responsible for the practice of collecting many cores then discarding all but a few which seem to give consistent trends, which many workers have done but which Sampson and Glock (1942) question. Regardless of the philosophical impropriety of the practice, the comparison of results from *Pseudotsuga* populations near Spokane with those near Moscow show quite clearly that certain groups of trees may reflect climatic influence whereas others do not. The same conclusion was reached by Lathe and McCallum (1939) who found that even when groups of 100 trees are used as a sample, some groups show no correlation with coordinate annual sequences that seem well-established by many other samples of equal size. Duff and Nolan (1953) likewise found a population of *Pinus resinosa* Ait. which, unlike other populations on less favorable sites, showed a conspicuous lack of synchrony. With so many interacting factors determining the sum of activity of the cambium, it may be that only rare individuals in a stand or rare stands escape erratic biotic and climatic influences so that their growth variations are determined principally by climate over a long period of years. Concordant sequences of thick and thin rings over a half century when exhibited by scattered trees must reflect weather even if such is observable in only a small percentage of individuals. It is interesting to note that even samples as large as 100 trees in the region north of Spokane may not show coordinate response to climate (Lathe and McCallum 1939), whereas as few as 5 trees may do so. Not far west of this region Hansen (1941) found 10-tree samples adequate.

Among the first to conclude that the thickness of xylem layers may not reflect weather conditions was Shreve who, after a study of *Pinus radiata* D. Don in California, wrote (1924): "The failure to find strong and uniform correlation between rainfall and growth in the wettest and driest years appears to be one of the most important pieces of evidence secured in this work against the possibility of using the growth record of trees as a universal criterion of rainfall conditions." Dobbs (1942) reached similar conclusions from his studies of *Larix decidua* Mill. in England; "Attempts to establish a pattern for annual ring-widths, on the lines originated by Douglass and co-workers in the southern United States, failed completely even with trees on the same site."

The conclusion now widely held among research

workers (Dobbs 1951, Hustich 1949) is that climatic control is reliably indicated by growth layers only in severe climates, *i.e.*, at the cold or dry limits of forests. From the present results, it must be concluded that there are exceptions even to this generalization.

If mature trees do not respond in their growth to water and heat variations at the ecologic limits of their distribution, it must be concluded that these limits are not related to the normal functions of mature individuals. Since viable seeds are produced at both limits, the most probable explanation of those limits involves the failure of germination or seedling survival. If this is true, here is striking evidence that the ecology of seedling and mature plants of the same taxon differs more than between comparable stages of different taxa.

Incidental Observations

The fact early became apparent that the width of xylem layers shows some rather consistent variations with the altitudinal positions of the trees. If one takes the widest layer in the pair of 50-year sequences representing a tree as a measure of maximum productivity, and this seems legitimate since most of the trees were not much older than this and all had passed the usual early period of rapid growth, the curious fact emerges that the two xerophytic trees, *Pinus* and *Pseudotsuga*, seem to find their highest growth potential at low altitude, whereas the two mesophytic trees, *Abies* and *Thuja*, can grow with equal rapidity at both ecologic limits of distribution (Table III). The t-test for significance of the differences in means shows that there is extremely low probability that the altitudinal difference is not as important as the means for *Pinus* and *Pseudotsuga* indicate, whereas there is very low probability that the small differences for *Abies* and *Thuja* represent more than sampling variation.

Table III. *Maximum thickness of xylem layers at opposed ecologic limits of distribution*

Tree	Mean of thickest xylem layer of 10 trees, 20 radii, in mm.	
	Low altitude	High altitude
Pinus	9.2	4.7
Pseudotsuga	7.7	3.9
Abies	5.3	6.4
Thuja	6.1	5.8

There is no apparent explanation for the above-described phenomenon, and it appears unrelated to the main problem of this research.

One further incidental observation seems worthy of mention. The number of light-colored sapwood layers is essentially the same at both the dry and cold limits of *Pseudotsuga* and *Thuja*. But at its cold limits, *Pinus ponderosa* sapwood varied from 64 to 120 or more layers in thickness, and the boundary between sapwood and heartwood was never very sharp, whereas along the dry limits the sapwood varied from 34 to 61 layers per tree, usually with a rather well-marked terminus. Thus, where the *Pinus* grows under relatively cool and moist conditions there is weak and delayed delayed development of heartwood. The wood of *Abies* shows no differentiation into sapwood and heartwood.

Acknowledgments

This investigation was supported in part by funds provided for biological and medical research by the State of Washington, Initiative Measure No. 171. I am also indebted to my wife for assistance with the field work.

Summary

In each of four taxa of trees (*Pinus ponderosa*, *Pseudotsuga taxifolia* var. *glauca*, *Abies grandis*, and *Thuja plicata*), wood layers were studied in individuals situated at the lowest and highest ecologic limits along the western edge of the northern Rocky Mountains near Moscow, Idaho.

So much discordance was found in the sequences of thick and thin layers along opposed radii of the same individual that no relationship between xylem formation and climate could be detected over a 50-year period.

These results are remarkable for the fact that although low-altitude individuals consistently grow more rapidly in early spring, then show more drouth shrinkage during the dry season, in comparison with high-altitude individuals, variations in the supply of heat and moisture during these seasons do not seem to affect the total amount of wood produced. The altitudinal relationship is thus different from the homologous latitudinal relationship in which temperature is said to become relatively more critical for tree growth in a poleward direction, and moisture more generally limiting in an equatorial direction.

The environmental factors which set upper and lower limits, therefore, do not measurably affect the total growth of mature individuals, but probably operate through control over germination or survival.

The two xerophytic trees, *Pinus* and *Pseudotsuga*, seem incapable of rapid diameter growth along their upper limits, but the two mesophytic trees *Abies* and *Thuja* can grow equally at either ecologic limit.

Along its upper altitudinal limits, the development of heartwood in *Pinus* is feeble and greatly postponed, but *Pseudotsuga* and *Thuja* show no difference in this respect.

References

Büsgen, M., and E. Münch. 1929. The structure and life of forest trees. John Wiley & Sons, N. Y. 436 p.

Cantlon, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. Ecological Monog. **23**: 241-270.

Daubenmire, R. F. 1946. Radial growth of trees at different altitudes. Bot. Gaz. **107**: 462-467.

———. 1947. Plants and environment. John Wiley & Sons, N. Y. 424 p.

———. 1949. Relation of temperature and day length to the inception of tree growth in spring. Bot. Gaz. **110**: 464-475.

Dobbs, G. C. 1942. A false-ring pattern in larch. Nature **150**: 377-379.

———. 1951. A study of growth rings in trees. Part I. Review and discussion of recent work. Forestry **24**: 22-35.

Duff, G. H., and Norah J. Nolan. 1953. Growth and morphogenesis in the Canadian forest species. Can. Jour. Bot. **31**: 471-513.

Flury, T. 1927. (The influence of drouth periods upon stand growth.) Mitt. d schweiz. Zentralanstalt f. d. forst. Versuch. **14**.

Glock, W. S. 1941. Growth rings and climate. Bot. Rev. **7**: 649-713.

Hustich, I. 1949. On the correlation between growth and the recent climatic fluctuation. Geografiska Annaler: 90-105.

Laitakari, E. 1920. Untersuchungen über die Einwirkung der Witterungsverhältnisse auf das Längen und Dickenwachstum der Kiefer. Acta For. Fenn. **17**.

Lathe, F. E., and A. W. McCallum. 1939. The effect of sufur dioxide on the diameter increment of conifers. p. 174-206 *in* Effect of sulphur dioxide on vegetation. Can. Nat. Res. Council, Ottawa. 447 p.

McMinn, R. G. 1952. The role of soil drought in the distribution of vegetation in the northern Rocky Mountains. Ecology **33**: 1-15.

Primault, B. 1953. (Relation of meteorological conditions to forest growth.) Schweiz-Zeitschr. Forstw. **104**: 524-534. (Biol. Abstr. **28**-9423).

Sampson, A. W., and W. S. Glock. 1942. Tree growth and the environmental complex: A critique of "ring" growth studies with suggestions for future research. Jour. Forestry **40**: 614-620.

Shreve, F. 1924. The growth record in trees. Carnegie Inst. Wash. Pub. **350**: 89-116.

THE SKIN AND RESPIRATORY WATER LOSSES OF *PEROMYSCUS MANICULATUS SONORIENSIS*

Robert M. Chew[1]

Department of Biology, University of Southern California, Los Angeles 7, California

The water that a small mammal loses from its body surfaces can be important ecologically. Excessive loss of water by evaporation may prevent water balance, while inadequate loss may interfere with heat balance, in specific habitats and niches. This has been demonstrated for *Dipodomys merriami* by the Schmidt-Nielsens (1951), and for *Peromyscus leucopus, Microtus ochrogaster* and *Blarina brevicauda* by Chew (1951). Chenoweth (1917) and Pruitt (1953) have shown the importance of moisture and evaporation in the ecology of *P. leucopus* and *B. brevicauda.*

In these studies of wild species, and in practically all water exchange studies of other mammals, only the total surface loss has been measured. There has been no direct separation of the total evaporation loss into its two components: (1) the skin loss—water that diffuses through the skin surfaces into the atmosphere, and also, in a few species, water that is secreted onto the surface, and (2) the respiratory loss—water that evaporates from the surfaces of the respiratory tract and is lost in the expired air. Therefore, the relative significance of each of these components is not definitely known.

Tennent (1946) made a few measurements on anesthetized white rats and reported that the skin loss was 57 per cent of the total evaporative loss. Since anesthetization is known to alter the rate of insensible water loss (the Schmidt-Nielsens in 1952 reported opposite effects of anesthetization on rate of evaporative loss to those of Tennent), it is doubtful whether this value can be extended to normal rats.

The Schmidt-Nielsens (1951) in their analysis of the water exchanges of *Dipodomys merriami* calculated the entire evaporative loss as coming from the lungs. Partly on the basis of these calculations they predicted that below a certain environmental relative humidity *merriami* would not be able to maintain water balance when given only air-dry food. When observations of experimental states agreed with these predictions, the Schmidt-Nielsens concluded that the skin water loss of *merriami* is insignificant. Similar experiments with the white rat indicated that for this form, "evaporation from the skin is not quite insignificant."

The present study of *Peromyscus maniculatus*

[1] Presented as a paper at the A.A.A.S. meetings at Berkeley, California, December 1954, under the sponsorship of the Western Society of Naturalists.

sonoriensis was initiated to determine directly the relative significance of the skin and respiratory losses of this ubiquitous subspecies of an ecologically important genus, and to test a method that may possibly be extended to other species and provide information for a comparative study.

I gratefully acknowledge the help of Mr. Joseph W. Bamberger who construced the flowmeters and head-lung chamber used in the apparatus.

Materials and Methods

The important part of the apparatus for measurement of surface water losses is shown in Figure 1. A 3/16-inch-thick balsawood collar was fitted snugly around the mouse's neck several days or weeks before the measurements in the chamber were made. While the collar limited the mouse's agility, it did not interfere with feeding or cause loss of weight. Just before the collared mouse was placed in the chamber, the collar was sealed to the skin with parloidion.

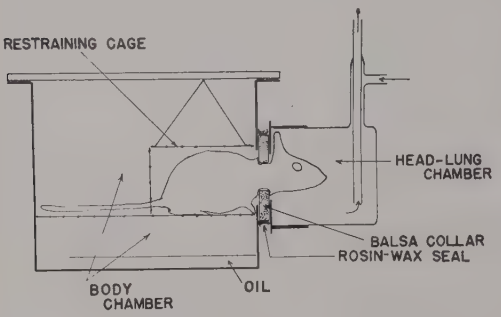


Fig. 1. Sectional view of animal chamber with partitioned mouse in place.

After the body of the mouse was inserted into the body chamber, the head-lung chamber, consisting of a modified 100-ml. beaker fitted into a metal base, was attached with four bolts, thus clamping the collar firmly in place and effectively partitioning the mouse into two sections. The collar and the glass plate topping the body chamber were sealed to the metal surfaces with a rosin-beeswax mixture. The balsa collars were impregnated with this wax in order to seal their pores, before they were attached to the mice.

The body chamber and head-lung chamber were components of separate Haldane-type open circuits. In operation 500 ml. of dry air was drawn through each chamber per minute, and the water vapor and carbon dioxide lost by the mouse into the outgoing air were collected in drying tubes containing Dehydrite and Ascarite. Air flow was checked on flowmeters in each circuit.

Urine and feces were collected beneath oil in the bottom of the body chamber so that water from these did not cause any error in the surface water-loss measurements.

After assembly of the apparatus, sixty-minute runs were repeated until two or more consecutive periods showed relatively constant values. Breathing rate, activity, alertness, and excitability were visually observed at intervals of 10-30 minutes during the measuring runs.

Repeated checks showed that the absorbing tubes functioned properly and that there was no leakage into the circuits from outside or between the two chambers.

Air temperature during the measuring runs averaged 26.8°C (standard deviation of 0.95°C), which temperature is presumably within the zone of thermal neutrality of this species, and is a temperature that *sonoriensis* encounters in part of its range during the hotter parts of the year. Relative humidity in the chambers averaged 6 per cent (2-13 per cent) during the measurements. The humidity was calculated from the water loss, using the formula of Batholomew and Dawson (1953).

The mice used were live-trapped in the Mojave Desert at Lovejoy Buttes, 15 miles east of Palmdale, California, in a community dominated by the shrubs *Larrea, Menodora* and *Hymenoclea* and abundantly populated by *Dipodomys merriami* and *Perognathus* sp.

Except when measurements were actually being made, the mice were kept in an animal colony room in which the temperature was relatively quite constant during any one week, but changed with the outdoor seasons from a weekly average of 19° to 25°C. Relative humidity in the room varied from 38 to 68 per cent. The mice were housed in no. 22 breadloaf-pan cages, and fed Purina Laboratory Chow.

Five series of measurements were made on the same group of eleven mice (reduced to nine near end by accidental deaths), Group A in Tables I and II, which were collected March 29, 1953. The mice were kept in the laboratory for five months before their surface water losses were measured, and during this time their food and water intake and activity patterns were measured (French 1954). One measurement was made on each of five other mice, Group B, collected February 27, 1954. All mice were adults and the females were not pregnant.

Measurements were made with the mice under three different conditions: (1) A1, A2 and A3 in Tables I and II, mice partitioned, postabsorptive (following 16-18 hours without food), and limited in their movements by use of a restraining cage, and with other precautions to keep metabolism

and evaporative losses to a minimum; (2) AC in tables, entire mouse within the body chamber, i.e. not partitioned; mouse postabsorptive, restrained, and without collar; (3) A4 and B in tables, mice partitioned, not postabsorptive, restraining cage not used, and mice deliberately disturbed at intervals in order to simulate maximum losses of a normally active mouse.

Measurements made under conditions (1) and (3) directly provide data as to the water loss of the skin of the body as separate from the water loss of the respiratory surfaces plus that of the skin of the head. Loss of water from the respiratory surfaces, as completely separate from any skin loss, was then calculated by the formula:

$$\begin{bmatrix}\text{respiratory}\\ \text{tract}\\ \text{loss}\end{bmatrix} = \begin{bmatrix}\text{measured mg.}\\ \text{water loss from}\\ \text{resp. tract and}\\ \text{head}\end{bmatrix} - \begin{bmatrix}\text{cm.}^2\text{ head}\\ \text{skin}\\ \text{surface}\end{bmatrix} \times \begin{bmatrix}\text{measured mg.}\\ \text{water lost/}\\ \text{cm.}^2\text{ body skin}\end{bmatrix}$$

From the removed skins of mice sacrificed at the end of the experiments, it was determined that 23.9 per cent of the total skin surface was anterior to the balsa collar, i.e. within the head lung chamber. The head skin surface area was then calculated as 0.239 x total surface area, the latter being taken as $9 \times Wt^{2/3}$. Water loss per square centimeter of body skin could then be determined as: (measured body skin water loss) ÷ (0.761 x total surface area).

These calculations depend on the assumption that the same rate of loss occurs for the skin of the head as for the skin of the body, which is not necessarily true. Different skin areas of *sonoriensis* may have different rates of loss, as found for human beings (Burch and Sodeman 1943); the ears, if thermally labile as in the dog (Hemingway 1938), may be extreme exceptions; and the moist conjunctiva undoubtedly has a higher rate of loss. Any error resulting from this assumption would probably be in the direction of exaggerating respiratory loss.

Results

Column I, Table I, summarizes the results of the direct measurements. As the measurements were repeated on the same mice (A1, A2, A3) there was a decline in the percentage of water lost through the skin of the body. This may have been the result of an observed, obvious decrease in the excitability of the mice as the experiments continued. In the first series of measurements the mice often gave evidence of excitement by persistently moving and tugging against the collar or by sitting with their legs braced against the collar or wire mesh. Some entire runs had to be discarded because the mice would not settle down, but this was not necessary in later series, as the mice sat quietly, usually with their eyes closed, and apparently relaxed, for at least two hours. Even the mice that were deliberately disturbed

Table I. *Data for skin and respiratory surface water losses of* Peromyscus maniculatus sonoriensis *at 26.8°C and 6% relative humidity*

Group and series designation	Date of measurements	Body weight, gm.	Body surface area, cm.²	Column I: Measured Body Skin Loss		Column I: Measured Head Skin + Respiratory Loss		Column II: Calculated head skin loss mg./hr./mouse	Column II: Calculated Total Skin Loss		Column II: Calculated Respiratory Loss	
				mg./hr./mouse	% total surface water losses	mg./hr./mouse	% total surface water losses		mg./hr./mouse	% total surface water losses	mg./hr./mouse	% total surface water losses
A1	9/1 - 9/15	18.2	62.2	34	48	37	52	11	45 (27-67)	63	26 (15-45)	37
A2	10/27-11/10	16.9	59.3	27	41	39	59	8	35 (25-43)	53	31 (21-40)	47
AC	11/25-12/3	17.6	60.9									
A3	1/6 - 1/20	16.4	58.1	18	35	34	65	6	24 (15-37)	46	28 (12-38)	54
A4	2/3 - 3/4	18.6	63.1	33	35	61	65	11	44 (31-73)	47	50 (36-69)	53
B	3/11- 4/8	18.7	63.4	48	47	55	53	16	64 (57-80)	62	39 (18-60)	38

All values, except the ranges given in parentheses, are group averages. Group A consists of 9-11 *sonoriensis* collected March 27, 1953; Group B consists of 5 individuals collected February 29, 1954.

Measurements were made under three different conditions:

(1) Series A1, A2 and A3—mice partitioned, postabsorptive, restrained in their movements, and with other precautions taken to obtain minimum values.

(2) AC—check measurements with the entire mouse, postabsorptive and not collared, within the body chamber.

(3) A4 and B—mice partitioned, not postabsorptive, not restrained, and periodically deliberately disturbed, in an attempt to simulate the maximum losses of a normally active mouse.

(A4) quickly became calm after each stimulus. Water lost through the skin of the body ranged from an average of 35 to 48 per cent of the total evaporatve loss.

The calculated skin: respiratory surface complete partitioning, Column II in Table I, shows a total skin loss ranging from an average of 46 to 63 per cent of the total evaporative loss. The skin: respiratory surface ratio for the deliberately excited animals (A4) was the same as that previously established for the same mice in a quieter state. Different mice experiencing the method of measurement for the first time (A1 and B) had similar skin losses of 63 and 62 per cent, which were conspicuously higher than the pecentages for the mice following experience with the method of measurement.

Table II gives the rates of loss in terms of metabolism, a logical method of expression favored by the Schmidt-Nielsens (1950). The rates of loss through the skin and respiratory surfaces varied both independently and in unison. In series A1 and A2 the total rate of loss is practically the same, but the partitioning is different; in A3 the total rate is less than in A2 due to a reduction in the rate of skin loss, while the respiratory loss remained unchanged; in A4 the total rate is greater than that of A3 but the partitioning is unchanged.

TABLE II. *Data for rate of skin and respiratory water losses of* P. m. sonoriensis *at 26.8 C. and 6% R. H. All values are group averages*

Group and series designation	ml. O_2/hr./gm. body wt.	Skin water loss mg. HOH/ml. O_2	Respiratory water loss mg. HOH/ml. O_2	Total surface loss mg. HOH/ml. O_2
A1	4.1	0.62	0.34	0.96
A2	4.0	0.50	0.43	0.93
AC	2.9	....	....	0.94
A3	3.8	0.39	0.44	0.83
A4	4.0	0.50	0.59	1.09
B	4.1	0.86	0.51	1.37

DISCUSSION

Few data are available as to the rate of metabolism of *Peromyscus*. Judging from the values of Pearson (1947) for subspecies other than *sonoriensis*, the values obtained for partitioned *sonoriensis* (Table II) are equal to those of moderately active deer mice, rather than basal metabolism values. The surface water loss data obtained are, therefore, more extensible to mice in the wild than would be information on mice in a state of minimal energy consumption.

Total surface losses of 52-103 mg. water/hr./-mouse, if extended over a 24-hour period, would amount to a daily total of 1.24-2.47 ml./mouse. Since water intake of the mice in Group A averaged 4.38 ml./day (2.65 ml. drunk, 0.56 ml. free water in food eaten, 1.17 ml. water of oxidation) according to French (1954), a surface loss of 1.24-2.47 ml./day would be 28-56 per cent of the total daily water loss of these caged mice. This is an important loss, which, for *sonoriensis* in their natural habitat, would have to be balanced by water in the foods eaten. Judging from work on *P. leucopus* (Chew 1951) this evaporative loss would be even greater, percentagewise, and more critical when natural foods are desiccated by the high temperature and low humidity of the desert in summer. Excessive evaporative loss may be a major factor in excluding *sonoriensis* from the driest parts of the desert, one of the few areas where this most widely ranging of California mammals is absent (Grinnell 1933).

None of the data indicate that the water loss from the skin ever reaches the point of insignificance. The directly measured loss through the skin of the body alone (76.1 per cent total skin surface) was, at its minimum, an average of 35 per cent of the total evaporative loss, while the calculated loss for the entire skin had a minimum value which was 46 per cent of the total.

Because of the constancy of the skin: respiratory surface partitioning in series A3 and A4, under different conditions of excitement of the mice, and different magnitude and rate of water loss, it is felt that a skin: lung partitioning of 46:54 represents what occurs for a mouse in the wild.

The data obtained are variable, but not unduly so for the processes involved. No very constant values were expected. Burch and Sodeman (1943) found that the vaporization from limited, isolated areas of human skin may vary markedly in the same person from time to time, even in consecutive 15 minute periods.

The data for *sonoriensis* indicate that in the present experiments the degree of emotional excitement is the most important reason for variability of the mean values for magnitude and rate of skin loss. Maximum skin loss was observed for that series of measurements when the mice were most excited, *i.e.* Series B, when the mice were first experiencing the method of measurement and were also deliberately disturbed and made active during the measurements. Minimum skin losses were obtained on the calmest animals, A3.

Just how excitation increases skin water loss is not at all clear. Speculatively the possibilities

are: (1) increased skin temperature, due to erection of the fur, heat released by active piloerector muscles, and/or increased peripheral blood flow, (2) increased hydration of subcutaneous tissue due to increased filtration through capillaries, (3) secretion of water.

Lung loss was greatest for the deliberately excited mice, probably because an immediate effect of each stimulation was a speeding of the breathing rate from about 110-140 to 240-250 breaths/minute.

The total rate of vaporization in series AC where the mice were neither partitioned nor collared was equal to or greater than that of the partitioned mice, and it is assumed that the partitioning did not cause any emotional increase in the rate of evaporation beyond that incident to keeping a wild mouse in a small container.

The relationship between water loss and rate of metabolism during individual measuring runs was analyzed. Typically, in a consecutive series of 60-minute periods, metabolism was greatest during the first hour, a relative minimum prevailed through the 2nd or 3rd to 4th or 5th hours, and metabolism then increased. The magnitude of the skin vaporization varied directly with this change in metabolism. Correlation indices calculated for the 39 60-minute runs composing the data of series A3 showed that the correlation of skin water loss with carbon dioxide production was significant at less than the 1 per cent level. The correlation of respiratory water loss and carbon dioxide was significant at the 5 per cent level.

The minimum rate of evaporative loss found for *sonoriensis*, 0.83 mg. HOH/ml. O_2 consumed (Table II), is similar to values of 0.85 and 0.94 found for the white mouse and rat respectively by the Schmidt-Nielsens (1950), but is 55 per cent greater than their average value for four species of desert rodents, e.g. 0.54 for *Dipodomys merriami*. It is likely that this is a real difference and that *sonoriensis* lacks a low evaporative rate as an adaptation for desert life.

Summary

A method is described for the separate determination of water losses from the skin and from the respiratory tract surfaces of small mammals. Data for measurements made at 26.8°C and 6 per cent relative humidity on *Peromyscus maniculatus sonoriensis* having a rate of metabolism of 4.0 ml. O_2/hr./gm. body weight show that:

(1) The total surface water loss of this species is an important one-fourth to one-half of its total water loss under laboratory caging conditions.

(2) Water lost through the skin of calm mice is an average of 46 per cent of the total surface loss, and therefore skin and respiratory tract losses are equally significant in the water economy of this animal.

(3) The magnitude and rate of the skin water loss, and less markedly, the respiratory tract loss, vary directly with the level of excitement of the mouse.

(4) There is a significant correlation between the magnitude of surface water loss and the amount of carbon dioxide produced.

References

Bartholomew, G. A. and W. R. Dawson. 1953. Respiratory water loss in some birds of Southwestern United States. Physiol. Zool., **26**: 162-166.

Burch, G. E. and W. A. Sodeman. 1943. Regional relationships of rate of water loss in normal adults in a subtropical climate. Amer. Jour. Physiol., **138**: 603-609.

Chenoweth, H. E. 1917. Reactions of certain moist forest mammals to air conditions and its bearing on problems of mammalian distribution. Biol. Bull., **32**: 183-201.

Chew, R. M. 1951. The water exchanges of some small mammals. Ecol. Monogr., **21**: 215-225.

French, R. L. 1954. Eating, drinking and activity patterns in *Peromyscus maniculatus sonoriensis*, under conditions of ad libitum and restricted water supply. Thesis. Dept. of Zoology, Univ. Southern California, Los Angeles. 81 pp.

Grinnell, J. 1933. Review of the recent mammal fauna of California. Univ. of California Pub. Zool., **40**: 71-234.

Hemingway, A. 1938. The effect of rate of heating and environmental temperature on panting threshold temperatures of normal dogs heated by diathermy. Amer. Jour. Physiol., **122**: 511-519.

Pearson, O. P. 1947. The rate of metabolism of some small mammals. Ecology, **28**: 127-145.

Pruitt, W. O. 1953. An analysis of some physical factors affecting the local distribution of the short-tail shrew (*Blarina brevicauda*) in the northern part of the Lower Peninsula of Michigan. Misc. Pub. Mus. Zool. Univ. Michigan, **79**: 1-39.

Schmidt-Nielsen, B. and K. Schmidt-Nielsen. 1950. Pulmonary water loss in desert rodents. Amer. Jour. Physiol., **162**: 31-36.

———. 1951. A complete account of the water metabolism of kangaroo rats and an experimental verification. Jour. Cell. and Comp. Physiol., **38**: 165-181.

Schmidt-Nielsen, K. and B. Schmidt-Nielsen. 1952. Water metabolism of desert mammals. Physiol. Rev., **32**: 135-166.

Tennent, D. M. 1946. A study of water losses through the skin in the rat. Amer. Jour. Physiol., **145**: 436-440.

EFFECT OF HEMLOCK AND RED PINE ON PHYSICAL AND CHEMICAL PROPERTIES OF TWO SOIL TYPES

François Mergen and Robert M. Malcolm[1]
Yale University, New Haven, Connecticut,[2]
and
British Columbia Forest Service, Victoria, B.C., Canada

Introduction

It has been recognized that forest tree species can exert an important influence on the fertility of the upper soil horizons. The degree of influence exerted depends largely on the amount of nutrients taken up from the soil and later returned in organic matter to the soil surface. In general, hardwood species absorb more nutrients from the soil and return a higher percentage of these nutrients in leaf fall than do conifers. However, the influence of species, age, and soil type, may cause variations from this general rule. For example, the litter of northern white cedar (*Thuja occidentalis* L.) contains more calcium that that of white oak (*Quercus alba* L.). Within the conifer group itself, there is considerable variation in the absorption of nutrients and their return to the soil. The rate and extent of decomposition of plant residues and the development of humus depends on the nature of the leaf litter reaching the forest floor, and on microclimatic factors such as surface soil temperature and moisture conditions. Decomposition is carried out by soil flora and fauna which consist largely of bacteria, fungi, earthworms, and mites. The nature of organic debris, particularly cell wall composition and calcium content of leaves directly affects the activity of these organisms and hence the rate of decomposition of organic matter and the type of humus produced.

In the northeastern part of the United States, hemlock (*Tsuga canadensis* (L.) Carr.) occurs naturally in mixed hardwood stands. Under suitable conditions, it grows well in competition with other species and regenerates naturally. Plantations with red pine (*Pinus resinosa* Ait.) have been established in various parts of New England, and the species has shown promise of high yields. In the State of Connecticut, however, it is growing at the southern extreme of its natural range and certain adverse biotic factors now appear to be operating against the species.

[1] Acknowledgment is given to Professor H. J. Lutz for suggesting this investigation and under whose direction it was carried out. H. I. Winer gave helpful assistance in the laboratory analysis.

[2] John A. Hartford Foundation Program in Forest Biology, Valhalla, New York.

In view of these facts, it seems that in the future more consideration will be given to growing hemlock on suitable sites, particularly in mixed hardwood stands. In this study, the influence of hemlock and red pine on certain important physical and chemical properties of the A horizon was determined on two soil types on which these two species were growing. These properties include volume-weight, pore volume, field capacity, air capacity, infiltration rate, pH, and calcium content.

Review of Literature

Ramann (1898) was one of the first foresters to investigate the influence of tree species on physical soil characteristics. He found a greater pore volume in the upper mineral horizon under beech than under pine and advocated underplanting beech in certain pine stands to improve soil fertility. Studies by Coile (1940) showed that the field percolation rates were significantly greater under stands of loblolly pine 20- to 70-years old, than those under a white oak-black oak-red oak forest type. He attributed the difference to a more favorable condition of the A_0 and A_1 horizons in the pine stands as compared with those in the oak forest. In the former, there were indications of relatively high activity of soil fauna, and considerable mixing of humus and mineral soil, whereas in the oak type the humus lay as a mat on the mineral soil, bound together by roots and fungus mycelia. Read and Walker (1950) investigated some physical and chemical properties of the surface soil under eastern red cedar (*Juniperus virginiana* L.) and red pine on two sites in Connecticut. They found that the calcium content and pH value of the upper part of the A horizon were significantly higher beneath eastern red cedar, than under red pine on both sites, and that pore volume and volume-weight were significantly higher under the cedar on one site only. They attributed the good physical condition of soil beneath eastern red cedar trees to the activity of earthworms. No earthworms were found in the surface soil under red pine trees.

Alway, *et al.* (1933) investigated the chemical properties of the unincorporated organic layers on soils under red pine, jack pine, white pine, and sugar maple-basswood forest types in Minnesota.

They found that differences in the ash, lime, nitrogen content, and pH values in these layers were small between jack pine and red pine, but large between these pines and the maple-basswood type. The soil under each forest type was similar and the authors attributed differences in the chemical properties of the organic layers to the influence of forest types.

Plice (1934) studied the content of calcium and other principal bases, antacid buffering, acidity, and total nitrogen content of fresh, mature, leaf litter of a number of coniferous and deciduous trees of the northeastern United States on various soils. He found great differences in these chemical properties according to species, and some variation within species on different soils, and observed a distinct influence of tree cover on the properties of the litter and the humus layers of the soil. Discussing the possibility of improving soil productivity, he stressed the importance of species composition of forest stands as related to soil structure.

Chandler (1943) analyzed the freshly fallen needle litter of eight conifers of the northeastern United States for mineral nutrient content. He collected litter of the various species from stands on two different soil types, and was able to show that the nutrient content of conifer foliage varied only slightly with change in soil type, but was closely related to species.

Lutz and Chandler (1949) advocated the retention of a small proportion of volunteer trees of "soil improving" species in forest stands, to utilize their production of litter high in content of bases and nitrogen. They expressed the view that it is possible and practical for a forester to regulate species composition in stands so as to favor the maintenance or slight improvement of soil fertility.

Experimental Procedure

Area of investigation

Two plantations were studied. The first called Plantation I, was on a level site adjacent to the northern tip of Lake Saltonstall, Connecticut. This site was used as a public recreation ground previous to planting. The plantation was on Branford sandy loam, a well-drained, brown podsolic soil which originated from stratified glaciofluvial deposits of Triassic sandstone and shale, mixed with some diabase, granite and gneiss.

The plantation consisted of 38 year-old red pine, stocked at about 630 trees pere acre, averaging 7.5 inches in diameter at breast height and 55 feet in height. In general, the trees were vigorous with well-formed crown, but gaps were in evidence due to the death of standing trees and to small patches of windthrow. Occasional hemlocks of natural origin were scattered thinly throughout the stand, and averaged 9 inches d.b.h. and 50 feet in height. These trees were establishd several years before the pines were planted, their average age being 44 years. They had larger crowns, particularly in the vertical dimension, than those of the red pine.

The total depth of unincorporated organic matter on the soil surface averaged 2 inches under the hemlock and 3 inches under the red pine. A thin black layer of unincorporated, but decomposed organic matter was more noticeable beneath the hemlock than beneath the pine.

Under both hemlock and red pine, the humus[3] was distinctly of the mor type, and there was little or no incorporation of organic matter in the A horizon of the soil under either species. No earthworms were observed, but there was considerable soil disturbance due to rodent activity in the unincorporated organic material and in the A horizon. The shrub and herbaceous vegetation, consisting of sparsely scattered individuals of *Sambucus racemosa* L., *Prunus pensylvanica* L., *Maianthemum canadense* Desf., and *Chimaphila maculata* (L.) Pursh was negligible.

The second plantation, designated Plantation II, was on a level site adjacent to the southeastern end of Lake Gaillard, Connecticut. Previous to planting, this soil was cultivated and fertilized with oyster shells. The soil type was Cheshire loamy sand, a brown podsolic soil derived from unstratified glacial till. The parent material was Triassic shale, sandstone, and conglomerate.

The forest cover consisted of two adjacent blocks; one was planted with hemlock and the other with red pine. Stocking was approximately 800 trees per acre in each block. The red pine was 24-years old and averaged 5.5 inches d.b.h. and 20 feet in height. The hemlock was 20-years old and averaged 5 inches d.b.h. and 25 feet in height.

The forest canopy in the hemlock block was extremely dense and a very low percentage of light penetrated to the forest floor. The canopy within the red pine block was considerably more open despite the presence of persistent low branches on most stems.

The total depth of unincorporated organic matter on the soil surface averaged one inch under the hemlock and 3 inches under the red pine. Under the pine, the A_F layer was made distinctive by the extensive growth of white fungus on the decaying

[3] Throughout this paper the authors adhered to the terminology and use of symbols relating to the organic matter and to the soil profile as defined in chapters 6 and 8 of "Forest soils" by Lutz and Chandler (1949).

needles. There was no true A_H layer below the red pine. Under the hemlock, no white fungus was observed in the A_F layer which was slightly deeper than under pine. A very thin true humus layer was present beneath hemlock.

Under both species, humus was of the mull type and the upper part of the A horizon was darkened by incorporated organic matter, forming a distinct A_1 layer. Earthworms were abundant in the A_1 horizon under each species. There was a marked concentration of very fine feeder roots at the surface of the A_1 horizon in the hemlock stand. Herbaceous vegetation was absent in Plantation II.

Field and Laboratory Methods

In each plantation, 5 pairs of hemlock and red pine trees were selected from various locations in the stand so that within each pair, the hemlock and pine were no further apart than 20 feet, the exact distance being determined by the requirement of having the crowns distinctly separated.

In Plantation I, the pairs were widely dispersed owing to the scarcity and scattered arrangement of hemlock within the plantation. In Plantation II, the pairs were located along the border between the hemlock and pine blocks. The distance between pairs was considerably greater than the distance within pairs. Care was taken to ensure that neither species of any pair was located close enough to a deciduous tree, which occasionally occurred in both plantations, for its litter to be appreciably influenced by the accumulation of deciduous leaves.

From 4 stations located at 3 feet from each selected tree and at approximately equal distances apart, soil samples from the upper part of the A horizon were collected in 1000 cc. metal cylinders, using the method outlined by Burger (1923). For the determination of the physical soil characteristics, volume-weight and pore volume, 4 samples were taken without altering the soil structure, and 4 more were collected for the determination of exchangeable calcium content and pH value. On undisturbed soil between these stations, 4 infiltration tests were carried out by means of the cylinder method, recording the time for one liter of water to infiltrate into the soil (Burger 1924).

The soil samples from each plantation were collected shortly after periods of heavy and continuous rainfall, so that they were approximately at their field capacity. All soil samples (160 in number) were carried to the laboratory immediately after collection. Those used for the determination of physical properties were weighed immediately on arrival, and then oven-dried to a constant weight. From the data thus obtained, a fairly good estimate of the field capacity of the soil under each selected tree was secured. Volume-weight, pore volume, and air capacity values were determined using methods described by Lutz (1944).

The 4 soil samples collected under each tree for the determination of chemical properties were air-dried and thoroughly mixed by using a riffle splitter. The composite samples thus obtained were passed through a 2 mm. sieve and subjected to chemical analysis in duplicate.

Exchangeable calcium was determined by analysis of ammonium acetate soil extractions using the method described by Peech, *et al.* (1947). The pH values of composite soil samples were determined by use of a Beckman meter equipped with a glass electrode.

In Plantation I, a rain gauge of the trough type with attached collecting drum was set up under each of the 10 selected trees to study the influence of hemlock and red pine crowns on the amount of precipitation which reached the forest floor (Fig. 1). The gauges were located at approximately 2 to 3 feet from the stem of each tree, at which distance they were well within the projected crown area. Stem-run off was not measured. The contents of the drums were measured at 2- to 3-week intervals. After each observation period, the rain gauge and drum were moved to a new location under the same tree crown with the aim of obtaining a fair average of rain penetration through the whole crown.

Using this technique, a series of data of the rainfall reaching the forest floor under 5 hemlock and 5 pine crowns were collected for 4 periods of varying rain intensity during March and April. For each period of measurement, the rain penetration figures were averaged separately for hemlock and red pine.

All chemical analyses were carried out in duplicate and the final determinations of soil properties were obtained by averaging these values. Determinations of physical and chemical soil properties were subjected to statistical analysis. Differences in soil properties discussed in the following sections are of statistical significance.

Results and Discussion

The data concerning physical and chemical properties of the soils studies are presented in Table I. The results of rain penetration measurements are presented in Figure 2.

In Plantation I, the only difference found between the surface soil under the two species was a slightly lower pH value beneath hemlock than

FIG. 1. Arrangement of trough rain gauges in Plantation I.

TABLE I. *Comparison of physical and chemical properties under eastern hemlock and red pine in two red pine plantations on the Eli Whitney Forest*

Property	Dimension	Plantation I		Plantation II	
		Hemlock	Pine	Hemlock	Pine
Volume-weight	Units	1.142	1.171^{NS}	0.970	1.020^{NS}
Pore volume	Per cent	56.05	54.64^{NS}	60.28	57.40**
Field capacity	Per cent	24.18	25.78^{SN}	30.71	30.43^{NS}
Air capacity	Per cent	31.83	28.85^{NS}	29.57	26.98^{NS}
Infiltration rate	Seconds	586	631^{NS}	170	535*
Calcium	Per cent	0.00698	0.01006^{NS}	0.07100	0.04366**
pH	Units	3.85	4.06*	4.16	4.13^{NS}

NS=not significant at 5 per cent level.
*=significant at 5 per cent level.
**=significant at 1 per cent level.

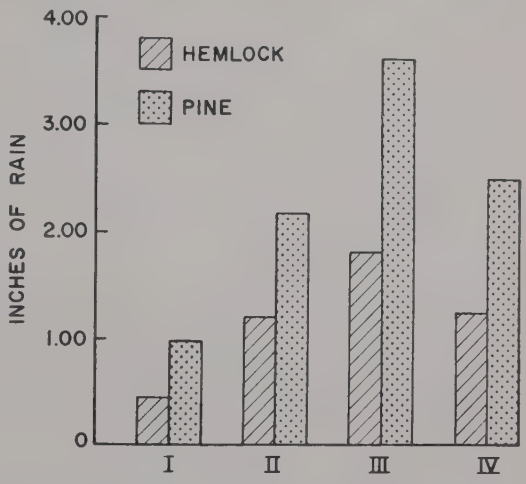


FIG. 2. Bar chart showing the results of rain penetration measurements under hemlock and red pine in Plantation I during four observation periods.

beneath red pine. There was no difference in the content of exchangeable calcium.

In Plantation II, there were considerable differences in physical and chemical properties of the surface soil beneath the two species. A greater pore volume, a faster infiltration rate, and a higher content of exchangeable calcium were found under hemlock than under red pine. The difference in volume-weight approached the 5 per cent level of significance.

The rain penetration data presented in Figure 2 show clearly that approximately twice the amount of rain, falling in storms of varying intensity, reached the forest floor beneath red pine compared with that beneath hemlock for the trees sampled.

In Plantation I, the pH value of the surface soil under hemlock was 3.85 and that under red pine was 4.06. This small difference, though of statistical significance, has little or no ecological significance. It may be considered as a reflection of

the slight difference in acidity in the foliage of the two species. Plice (1934) recorded pH values of 3.7 and 3.3 for hemlock litter and 4.15 for that of red pine.

The absence of any difference in the physical properties of the surface soil beneath the two species in Plantation I is attributable to their raw humus which presented unfavorable conditions for earthworms. However, the lack of earthworms may be related to the low calcium content of the unincorporated organic layers and surface soil, as well as to the low pH values in these layers. Read and Walker (1950) observed earthworms in a soil with a pH value of 4.76 where the calcium content was 0.108 per cent, but not in a soil where the pH value was 4.08 and the calcium content 0.014 per cent. It has long been recognized that earthworms, by mixing organic matter and mineral soil, favorably influence the pore volume and other physical properties of the soil. Bornebusch (1930) recorded that earthworm activity in certain Danish mull soils was responsible for their friable structure. He also recorded the sparseness of earthworms in raw humus.

The results of the experiment do not permit any conclusions to be drawn regarding the relationship between the chemical and physical properties of the soil and the rain penetration through hemlock and red pine. However, the data in Figure 2 strongly indicate that the organic matter and surface soil under the greater part of the hemlock crowns are, in effect, under the influence of a microclimate which is approximately twice as dry as that under red pine. In considering the fact that the A_0 layer was deeper under red pine than under hemlock, it should be pointed out that the more favorable moisture conditions for decomposition may have been offset by the greater age of the red pine needles and their consequent slower decomposition than hemlock needles. According to Harlow and Harrar (1941), red pine needles persist on branches until the fourth or fifth season but needles of eastern hemlock persist only until the third season. Albert (1928) reported an increase in the rate of decomposition of tree litter with a decrease in the number of seasons that the leaves remain on the branches.

Considering the results obtained in Plantation I, it may be stated with justification that hemlock has not brought about any soil deterioration of ecological significance in the red pine stand.

The most striking difference in Plantation II was in the calcium content of the surface soil. The A_1 horizon under hemlock contained 0.071 per cent available calcium whereas that under red pine contained only 0.044 per cent. The base exchange capacity of the F layer is a factor of great importance influencing the nutrient content of the surface soil. Wilde, *et al.* (1937) reported that the F layer of eastern hemlock has a base exchange capacity of 73.2 m.e. and a replaceable calcium content of 29.4 m.e., whereas the F layer of red pine has a base exchange capacity of 29.3 m.e. and a replaceable calcium content of 12.9 m.e. It is probable that a greater base exchange capacity of the A_F layer under hemlock in Plantation II contributed to the higher content of replaceable calcium in the A_1 layer under the species as compared with that under red pine.

The soil in this plantation was cultivated and fertilized with oyster shells and possibly with other organic material, prior to planting. Hence it is fairly certain that there was a satisfactory distribution of soil macronutrients. Eisenmenger (1950) stated, "the greater the number of useful cations in the nutrient solution, the more favorable is the condition for intake." His view was based on the concept of ion antagonism. Considering the high probability of this condition being favorable in Plantation II, the opportunity for the species to influence the calcium content of the surface soil beneath them was good.

Despite the considerable difference in the calcium content of the A_1 horizon under hemlock and red pine, there was no difference in their pH values. There seemed to be little or no relationship between the calcium content and pH values of the surface soil in this plantation. Other investigators have recorded data which corroborate this finding. Plice (1934) studying chemical properties of tree litter, found no consistent relation between the base content, antacid buffering, and acidity of the litter of a large number of tree species including hemlock and red pine.

The higher pore volume and faster infiltration rate of the surface soil under hemlock reflected its higher calcium content. Baver (1936) expressed the view that the beneficial effect of calcium ions in the soil is due to their indirect effect of causing flocculeş which may be bound together into stable aggregates by organic matter. Laatsch (1938) emphasized the favorable influence of calcium on life conditions for soil organisms which incorporate organic matter in the A horizon. He stated that a moderate amount of calcium is the prime condition for the maintenance of a stable crumb structure.

Summary

1. The influence of hemlock and red pine on volume-weight, field capacity, air capacity, infil-

tration rate, pH, and exchangeable calcium content of the soil was studied on Branford sandy loam and on fertilized Cheshire loamy sand.

2. The results show that on the Branford sandy loam, the only effect of species on the soil was a slight lowering of the pH under hemlock as compared with that under red pine. On the fertilized Cheshire loamy sand, where the level of exchangeable calcium was several times higher, the pore volume, infiltration rate, and calcium content of the surface soil under hemlock were more favorable than under red pine.

3. The view was expressed that the content of exchangeable calcium in the surface soil was the most important single factor tending to bring about a favorable physical condition of the soil.

4. On the two sites investigated, no evidence was found to show that red pine is preferable to hemlock in regard to the maintenance of soil fertility.

References

Albert. 1928. Die sogenannten Bodenerkrankungen, ihr Wesen, ihre Ursache und Bedeutung für die Forstwirtschaft. Jahresbericht des deutschen Forstvereins **1928**: 118-119.

Alway, F. J., Kittredge, Jr., and W. J. Methley. 1933. Composition of the forest floor layers under different forest types on the same soil type. Soil Sci. **36**: 387-389.

Beaver, L. D. 1936. Aggregation of soil and calcium ion saturation. Amer. Soil Surv. Assn. Bull. **17**: 28-30.

Bornebusch, C. H. 1930. The fauna of forest soil. (Skovbundens Dyreverden) Det forstlige Forsøgsvaesen i Danmark **11**: 1-158.

Burger, H. 1923. Physikalische Eigenschaften der Wald- und Freilandböden. Bühler Buchdruck, Zürich. 221 p.

———. 1924. Die physikalische Bodenuntersuchung, insbesondere die Methoden zur Bestimmung der Luftkapazität. IV Internationale Konferenz für Bodenkunde. Abt. I-A; Nr. **2**. 14 p.

Chandler, R. F. Jr. 1943. Amount and mineral nutrient content of freshly fallen needle litter of some northeastern conifers. Proc. Soil Sci. Soc. Amer. **8**: 407-411.

Coile, T. S. 1940. Soil changes associated with loblolly pine succession on abandoned agricultural land of the Piedmont Plateau. Duke Univ., School of Forestry Bull. **5**: 85 p.

Eisenmenger, W. S. 1950. Relative capacity of soils to furnish ions to plants. Jour. Forestry **48**: 416-418.

Harlow, W. M., and E. S. Harrar. 1941. Textbook of dendrology. McGraw-Hill Book Co., New York. 542 p.

Laatsch, W. 1938. Dynamik der deutschen Acker- und Waldböden. Theodor Steinkopff Verlag, Dresden und Leipzig. 270 p.

Lutz, H. J. 1944. Determination of certain physical properties of forest soils. 1. Method utilizing samples collected in metal cylinders. Soil Sci. **57**: 475-487.

Lutz, H. J., and R. F. Chandler, Jr. 1946. Forest soils. John Wiley and Sons, New York. 514 p.

Peech, M., L. T. Alexander, and L. A. Dean. 1947. Methods of soil analysis for soil-fertility investigations. U.S.D.A. Circ. No. **757**. 25 p.

Plice, M. J. 1934. Acidity, antacid buffering, and nutrient content of forest litter in relation to humus and soil. Cornell Univ. Agr. Exp. Sta. Mem. **166**. 32 p.

Ramann, E. 1898. Der Einfluss verschiedener Bodendecken auf die physikalischen Eigenschaften der Böden. Zeitschr. f. Forst- und Jagdwesen **30**: 451-483.

Read, Ralph A., and Laurence D. Walker. 1950. Influence of eastern red cedar on soil in Connecticut pine plantations. Jour. Forestry **48**: 337-339.

Wilde, S. A., S. F. Burnan, and H. M. Galloway. 1937. Nutrient content and base exchange properties of organic layers of forest soils in the Lake States region. Soil Sci. **44**: 231-238.

STUDIES FROM THE AUTOTREPHON, III. A BLACK MUTATION OF *TRIBOLIUM CONFUSUM* COMPARED WITH THE NORMAL REDDISH-BROWN STRAIN

John Stanley and H. M. Slatis
Departments of Zoology and Genetics, McGill University, Montreal, Canada

Introduction

This paper discusses in detail the life history of the normal reddish-brown strain of *Tribolium confusum* Duval living at 30°C., and 75% Relative Humidity, in whole wheat flour, plus 3% of ground wheat germ. It compares this life history with that of a black mutation of the same insect, reared under as closely as possible, identical conditions. Observations were made with the aid of the autotrephon (Stanley 1951, 1953a, 1953b), an apparatus for the automatic rearing of insects, with time-controlled withdrawal of samples.

Origins of the Stocks

The normal reddish-brown insects, hereafter referred to as "McGill Red," or simply "red," were descendants of the stocks maintained by R. N. Chapman at the University of Minnesota in the 1920's and 1930's. This stock was used by Chapman for his long series of papers on population

growth, and by Chapman and Baird (1934) for their valuable paper on the biotic constants of *Tribolium confusum*. A subculture was imported into Canada by one of us (J.S.) in 1932, and has been maintained under substantially constant conditions since that time. During the period 1941-1946, owing to the war, cultures had to be left with only occasional changes of flour. The food medium has always been whole wheat flour plus 3% of ground wheat germ. Flour has been obtained from various sources, as available, but in recent years, Ogilvie's "'C'-stream, unbleached" has been used.

McGill Red has been checked against sundry wild strains, obtained from mills and ships, in Montreal and elsewhere. While the remarkably discriminating technique of the autotrephon does show some very small significant differences between the life history of McGill Red and each wild strain (and between all the wild strains, too), the differences are very small indeed, and show no consistent trend. It is felt that, for all practical purposes, one can say that McGill Red, as it now exists, does not differ to any worthwhile degree from an average wild strain. It is largely a 6-instar strain. Indeed, until recently, it was thought to be fully so, but we have recently found a few 7th-instar larvae, and a very few 8th-instar. This somewhat spoils the accuracy of the determination of the point (6-P), where 50% of the larvae transform to pupae. This point will be discussed later. At the time the data for this paper were collected, the technique used could not detect these few higher-instar larvae.

The mutation, McGill Black, is an intensely black form, discovered in the cultures in 1950 by Miss Helen J. Martin, Research Assistant to J. S. at that time. A pure culture was isolated, and has been since maintained. As will be shown later, McGill Black is not the same as the mutation "ebony," described by Park, Ginsberg and Horowitz (1945).

Literature

It is somewhat surprising, in view of all the work which has been done with *Tribolium confusum* (particularly in connection with population studies), that there is so little really sound information as to its exact life history. In point of fact, though there are many papers which give fragmentary data for various foods and temperatures, there are only 3, to the writer's knowledge, which give clean-cut constants with reasonably small variance.

Sweetman and Palmer (1928) used the insect as a test animal for vitamin research, and showed that the addition of brewer's yeast and wheat germ to the food reduced the time required for development. They obtained times varying from 20.8 days (499.2 hr.) to 30.6 days (734.4 hr.) from egg to adult at 28°C. However, the instars are lumped for the larvae.

Brindley (1930) published data for the durations of the various stages, including larvae, at 29.7°C., but the Standard Errors are not shown.

Chapman and Baird (1934) made a most careful study of *Tribolium confusum* and their sets of biotic constants at 17°, 22°, 27° and 32°C., form the main part of our knowledge in this field. Rearing was done in the ordinary way by hand. It would appear from their discussion that eggs were examined hourly, the other stages daily. If we compute as closely as possible the means and Standard Errors of the data of Chapman and Baird, we have approximately: eggs, 105.84 ± 0.312 hr.; lumped larvae, 416.40 ± 1.88 hr.; pupae 128.88 ± 1.91 hr. at 32°C. The roughly comparable values from this present paper for Combined Reds at 30°C., calculated from Table III, are: eggs, 116.31 ± 0.63 hr.; lumped larvae, 418.37 ± 1.85 hr.; pupae 142.52 ± 1.91 hr. The actual values are not really comparable, owing to the 2-degree difference in temperature, but the Standard Errors are of interest. They are of about the same order of magnitude in both cases, and bear testimony to the excellence of the work of Chapman and Baird. It might be remarked, though, that had these authors continued hourly observations throughout the life history, the effort involved would have been formidable.

Stanley (1946) published a paper combining some of his own data with that of Chapman and Baird (1934) and obtained smoothed values for various temperatures by interpolation. The instars are lumped and no Standard Errors are shown. In general, the data, though showing interesting trends with temperature, are not reliable in individual cases.

If one compares the data of Stanley (1946) at 30°C., with those of this present paper, it will be found that in every case the values of 1946 are higher than those shown here. For example, we have for eggs, larvae and pupae successively, in 1946: 117, 482 and 160 hr. The present values are 116.31, 418.37 and 148.52 for Combined Reds, as in Table III.

Part of the discrepancy is clearly due to the natural difficulties of curve fitting, but much of it is believed to be due to the effect of considerable disturbance in hand rearing and almost zero disturbance in autotrephon rearing. Chapman and Baird mention that disturbance lengthens the life

history, and they made every effort to minimize it. They could not, however, eliminate it, and it will be noted that while the autotrephon can rear larvae from egg to pupae in 418+ hours at 30°C., the hand rearing of Chapman and Baird at 32°C., shows an acceleration of only 2 hr. A rough calculation from an autotrephon run at 32°C., shows an acceleration of about 40 hr., giving a lumped-larvae development time of about 366 hr.[1] Reynolds (1945) mentions a similar effect of retardation, if *Tribolium destructor* is disturbed.

In the autotrephon there is of course no disturbance at all, other than the faint hum of the air-conditioning system, and this laboratory has invariably found that life histories from the autotrephon are shorter than those found in the literature. It is not intended to discuss this matter fully here, but it may be mentioned that one extremely carefully controlled experiment showed that simple daily shaking of the vials would lengthen the life history from approximately 683 hr. to about 716 hr. at 30°C.

Technique

The experiments leading to this paper were done in two sets, the genetical part by H.M.S. and the life-histories by J.S. There is nothing unusual that needs discussion as far as the genetical technique is concerned. The insects were reared in vials at 30 ± 0.1°C., and 75 ± 2.0% Relative Humidity,[2] in the laboratory's standard flour plus 3% of wheat germ. The autotrephon could not be used for this part of the work, as it is not adapted to it.

For the life histories, the samples were housed in either glass or plastic vials. It was thought initially that insects developed faster in plastic than they did in glass, perhaps due to some volatile substance diffusing from the plastic and affecting growth. It is now known that the apparent acceleration is due to freedom from disturbance, as explained above, and there is no evidence of any acceleration due to rearing in plastic.

The food used was Ogilvie's "'C'-stream, unbleached" whole wheat flour, sifted to pass 100% through a 60-mesh bolting cloth. The 3% of wheat germ was intimately mixed in, using a ball-mill with a reduced load of pebbles. Each sample-vial held 30 gm. of the flour, with a variation of ± 0.1 gm. The flour was weighted in after allowing it to come into equilibrium with 30°C., and 75% R.H. This weight of flour has a volume of almost exactly 60 cc.

[1] This is rough figure for illustration only, and subject to small change on LD_{50} analysis.

[2] The use of the sign ± here indicates merely the limits of random variation about the mean value.

In each vial the flour was seeded with 25 new-laid eggs obtained by sifting a large culture once (to clear out old eggs), and then sifting again 2 hr. later. The spread of the ages about the mean is thus ± 1.0 hr. If we assume that the eggs are laid at a uniform rate throughout the 2-hour interval, the eggs would be distributed about a mean age with a Standard Error of ± 0.12 hr. We cannot however be at all certain of such a uniform rate. Probably eggs are not laid at once after the first sift, and the true Standard Error must be more than the theoretical. We have no way at present of determining it, and as a compromise, it has been arbitrarily given a value of ± 0.5 hr.

The instant of laying is then taken as midway between the two sifts and, for example, in the case of Experiment Red-1, the first sift was at 9.00 A.M. and the second at 11.00 A.M. The eggs then all date from 10.00 A.M., and start with a mean age of 0.00 ± 0.5 hr. The choosing of any other reasonable value for the Standard Error of the starting instant does not affect the end results, and ± 0.5 hr. is the writer's best estimate of a suitable value.

The use of a Standard Error for the starting instant does not affect the value of the point (E-1), when 50% of the viable eggs have hatched, but it does affect the calculation of the time *spent as an egg*. It is for this reason that (E-1) appears as 116.86 ± 0.87 hr. in Table III, while the time spent as an egg appears as 116.86 ± 1.00 hr. in Table VI.

By the use of radiant heat the eggs were kept as close as possible to 30°C. while being counted out, and every effort was made to avoid any but brief exposures to other temperatures during manipulation of the samples in loading etc. The temperature control in the autotrephon was accurate to ± 0.05°C., and the relative humidity to ± 0.5°C., wet-bulb temperature. In view of the insulating effect of the flour surrounding the insects, this represents almost perfect control.

With occasional exceptions, the samples were released exactly on time. Where mechanical failures made a sample late, this was taken into account in the calculations. The recording system of the autotrephon marks the exact time of release.

The autotrephon experiments were not performed specifically for this paper. Rather the limits and coverage of the paper were decided, and suitable data were then withdrawn from the files. It follows that experiments were spread over several years. Altogether 5 life histories are described, 3 for McGill Red and 2 for McGill Black. These experiments were as follows:

Red-1. This is the experiment previously described in Stanley (1953b). It is included here partly to show the consistency of the results obtainable with the autotrephon, and partly to compare the results obtained by the graphical method of Stanley (1953b) with those from the more elegant LD_{50} technique of this present paper. The experiment began on Monday, February 27, 1950. It was intended to sample every 5 hrs., as it was not clear at that time what was the best sampling interval. Certain mechanical difficulties intervened with the then new apparatus, and the sampling intervals were not always correct. However, the actual times were used for calculation. Instars were determined by micro-metric measurement across the two eyes (outer boundary to outer boundary), using Dyar's Rule (1890). This experiment was housed in plastic, and the short life history, only 681.5 hr., led to the suspicion that there was some acceleration from rearing in plastic. Stanley (1946) had shown 729 hr. as a calculated life history time at 30°C.

Red-2, Red-3, Black-1 and Black-2. In an attempt to check the possibility of acceleration in plastic *versus* glass, these were done as a quadruple run, using "linked" tracking in fours (Stanley 1953b), so that a set of all four kinds was withdrawn every 10 hr. Red-2 and Black-1 were in plastic, Red-3 and Black-2 in glass. As stated, the acceleration in plastic is a myth. The instar determination was substantially as in Red-1, with somewhat better discrimination. The run commenced on November 28, 1951.

Analysis of the Data

Experiment Red-1 was analysed in Stanley (1953b), using a graphical method for finding the points (measured in hours from the mean time of laying) at which 50% of a given stage had transformed to the next successive stage. This method is simple and easy to carry out, but it does not provide any Standard Errors, and so the significances of differences cannot be determined.

A little thought showed that what was really being done was to "dose" the insects with increasing amounts of time. Therefore the well-known "LD_{50}" technique, used to assess the effects of varying doses of poisons, should be applicable. Instead of insects being dosed with poisons, and 50% dying, insects are dosed with "time" and 50% transform. This method was introduced by Bliss (1935a, 1935b), but the discussion in Bliss is not simple. That of Mather (1947) is clear and easy to understand, and Mather's method was used exclusively.

Space hardly permits the inclusion here of a worked-out example, but the method is briefly this. Percentages of insects transformed at each observation are changed to probits, and these probits are plotted as ordinates against time. If all is well, the plot will be roughly a straight line. If it is curved, a logarithmic or other transformation may be used to straighten it. A straight line is then fitted to the plot by eye, or if desired, by a straightforward least squares fit, without any weighting of the observations. New "fitted" values of the probits are then taken from this line, and used to fit a new line by a weighted least squares fit, using weights taken from a table.

The subsequent calculation then finds the equation of this new line, and finds "LD_{50}," the abscissa for which the ordinate is 50%. Obviously, the final line must be a valid fit to the data, and the excellence of agreement can be checked by calculating Chi-square, as per Bliss (1935a).

In pharmacological work, logarithmic transformations are often necessary to make Chi-square sufficiently small. In the case of the transformation of beetles to a further stage, it is probable that the time scale does not directly reflect the actions of the forces which operate in ontogeny. It is reasonable to suppose (and this seems to be borne out by observations) that there is less likelihood of a beetle being precocious than there is of its being slow. The laggards will have a distinct effect in drawing out the central part of the plot towards the later parts of the time-scale, making some calculations of LD_{50} yield values which are too large. This source of error was not taken into account (*i.e.* logarithmic transformations were not made) for a number of reasons. The major reason is that observation suggests that the effect cannot be great, as laggards are not common. Confirmation of this view is derived from Table I, which compares the values determined graphically with those from the LD_{50} analysis.

Inasmuch as the graphical method was not

Table I. *A comparison of the values for the transformation points in Experiment Red-1, obtained by the graphical and LD_{50} methods*

Trans. point	Time value in hours		Diff. hrs.
	Graph.	LD_{50}	
E-1	115	116.86±0.87	+1.86
1-2	146	146.84±1.05	+0.84
2-3	225	224.85±0.79	−0.15
3-4	287	285.56±1.28	−1.44
4-5	344	345.24±1.19	+1.24
5-6	409	410.15±0.81	+1.15
6-P*	528	527.51±2.24	−0.44
P-A	683	681.51±1.62	−1.49

*A few 7th and a very few 8th instars are present. This point might be called (L-P), meaning 50% larvae transformed to pupae.

affected by any asymmetry about the 50% point, it can be assumed to be free from any bias due to failure to transform the scale. The obviously random distribution of the discrepancies of Table I indicates that no particular bias existed which would consistently affect the value of LD_{50}.

Another excellent reason for refraining from transforming the time scale was the lack of any reasonable formula for making such a transformation. The study of enormous numbers of beetles would doubtless result in empirical factors for the correction of observations, but these would be of value only in the particular case for which they were determined.

Bliss (1935a) describes two methods for this Chi-squared check, and the data for Red-1 for all transformation points except (E-1) were tested by the easier method. Four of the Chi-square values were not significant, two were significant at the 5% level, and one, that for the transformation from 6th instar to pupae, was significant at much less than the .001 level. This case showed some markedly deviant samples, and is discussed below.

If this single instance of a highly significant Chi-square be removed from the data, the other values of Chi-square may be tested together by adding the Chi-squares and the degrees of freedom. The total Chi-square was found to be 36.7 with 24 degrees of freedom, for which the probability is almost exactly 0.05, a not unreasonable result. The use of Chi-square for this test was greatly limited by the fact that there are biases in both the data and the analyst which affect the value of both Chi-square and the number of degrees of freedom.

We now consider the value of Chi-square for the point (6-P). At the time this paper was first written, it was thought that there were no more than 6 instars, and that the transformation from 6th instar to pupae was just that. Further work with other autotrephon runs, combined with a new technique for instar determination (to be described in a later publication) shows that under some conditions there may be a few 7th instars, a very few 8th, and even an occasional 9th instar, though these last are rare indeed. These higher instars are larval laggards beyond the time (6-P) and they spoil the form of the percentage and probit plots in this region, increasing the Chi-square. In reality, there are times such as (6-P), (6-7), (7-8), (8-9) and (7-P), (8-P) and (9-P). The point called (6-P) in this present paper is a sort of weighted mean of (6-P), (7-P), (8-P) and possibly (9-P). It might be better to call it (L-P) meaning "the point at which 50% of the mature larvae have pupated." Data are not available for the present experiments to improve the situation, but subsequent publications will deal with it in detail for later experiments.

The resultant haziness in (L-P) is not serious for *Tribolium confusm* at 30°C. in whole wheat flour, because 7th and 8th instars are rare, and 9th virtually unknown. Indeed, the Standard Errors shown in Table III are pleasingly small for biological material. For *Tribolium castaneum*, however, the problem is more serious, as a fair proportion of 6th instar go on to the 7th, many of these then go to the 8th, but 9th are very rare.

Although, from the point of view of elegance (whatever that may mean), the LD_{50} technique is perhaps the method of choice, it does not, in the case of autotrephon data, yield transformation points which are appreciably better than those obtained by the graphical method. Table I shows the values of the successive points in the life history of Red-1 obtained by both methods. It will be observed that the maximum difference between the two is 1.86 hr., for the point (E-1), and this is only just significant. In view of the fact that, with ordinary "hand" rearing and daily observations, the Standard Error may be as much as $\pm$ 12 hr., a discrepancy of 1.86 hr. is negligible.

It must be remembered also that this discrepancy arose in Red-1, an experiment performed when our rapidly improving technique for instar-determination was in its infancy. Plots which we can now produce are so smooth that there is no difficulty whatever in making a very exact determination graphically. For a run now being analysed the calculation time, using LD_{50} and some other analysis, is already over 90 hr., and some 50 more will be needed. The same thing could be done graphically with only nominal loss of accuracy in some 5 hr. work. Admittedly the Standard Errors would be lost, but unless values in pairs are very similar, statistical confirmation of significance is hardly necessary. For example, *T. castaneum* reared at 28°C. and 65% R.H. is approximately 40 hr. faster than *T. confusum*. The Standard Errors of the respective transformation points are certainly not greater than $\pm$ 1.5 to 2.0 hr. No elaborate analysis is needed to convince the experimenter that *castaneum* is winning the race in such a case.

It might be added here that the points (E-1) were found exactly as in Stanley (1953b), using a preliminary curve for egg-hatching obtained from an egg-timer (Stanley 1939), and making subsequent compensation for egg-mortality. In practice, in future, it is intended to determine (E-1) entirely from the egg-timer data, discard-

ing the first-instar and egg curves from the autotrephon. The first-instar are difficult to deal with, and less than 25 are available, whereas 500 or more are easily handled on one pass of the egg-timer, and timing is good to the nearest 0.25 hr.

It will be seen from what follows that all the life histories are very similar. So much so that it has been a matter of some difficulty to find any means of pictorial presentation which will adequately display them. Certain possible methods are shown later, but the writers are open to suggestion as to better methods.

The writers make no apology for these perhaps somewhat halting adventures in statistics. They are still very much feeling their way with the analysis of autotrephon data, and must use such methods as they can devise. They are open to suggestions as to some statistical method of dealing with a pair of life-histories *en bloc*. The piece-meal dissection of life-histories by a succession of LD_{50}'s does provide interesting information as to trends as time marches on, but it does not really answer the crucial question: "Are these two life-histories in essence the same, or do they differ, and if so, how, and to what extent?" Figure 2 provides at least a crude answer. Very large quantities of raw data are available to anyone who cares to investigate this problem.

Discussion

Genetics

The genetics of the black coloration in McGill Black *Tribolium confusum* have been studied in the Department of Genetics at McGill University by H.M.S., who has also investigated a similar mutation in *Tribolium castaneum*, to be described later.

Crosses of McGill Red & McGill Black produce an intermediate form, slightly darker than the normal red, with a peculiar faint bronzy iridescence. The name "bronze" is suggested for this form. The distinction between red and bronze is not as marked in *T. confusum* as it is in *T. castaneum*.

The F_1 bronze beetles were crossed to yield 59 red, 134 bronze and 51 Black in the F_2 generation. The value of Chi-square is 2.89 and $P > 0.2$ (2 d.f.) so that this result does not differ significantly from that expected on the assumption that black is a simple semi-dominant mutation. Various crosses of F_2 beetles were made, and the data are shown in Table II. The results agree with the hypothesis that black is a semi-dominant mutation. However, the observed number of black offspring in the cross: bronze x black, is much smaller than that expected, the chance of such a discrepancy being less than one in one thousand. A similar deficiency of blacks in the cross of bronze x bronze is not quite statistically significant.

Table II. *Progeny from various croses of* F_2 Tribolium confusum

Cross	No. of crosses	Number of various colors		
		Red	Bronze	Black
Red x Red	2	76	0	0
Red x Bronze	2	31	19	0
Red x Black	1	0	49	0
Bronze x Bronze	1	5	11	0
Bronze x Black	9	0	96	55
Black x Black	1	0	0	41

These discrepancies might be due to any one of three causes: (a) faulty classification of a red parent as bronze, (b) lower viability of blacks (though this is not shown by later rearings in the autotrephon) or (c) a chance variation. It will be noted that the counts of the F_2 beetles also give a smaller number of blacks than expected, though the deficiency is not quite statistically significant, and in this case there cannot be any question of faulty classification. There is therefore some reason to believe that, in the genetical experiments at least, black beetles were not as viable as red or bronze. It has been shown by certain of the above crosses that there is no linkage between black body-color and sex.

A recessive dark body color, "ebony," represented by *ee*, has been reported for this species by Park, Ginsberg and Horowitz (1945). They describe the color as "nearly black to the eye." Through the kindness of Dr. Thomas Park, at the University of Chicago, a culture of ebony *T. confusum* was made available to the writers, who compared it and crossed it with McGill Black, though no life histories were examined.

When McGill Black is crossed with ebony, the progeny are all bronze, or at least no darker than one would find in a cross of black x red individuals. In the F_2 generation, the progeny were identified as 44 red, 102 bronze, 37 probably ebony and 44 as probably black. The occurrence of red beetles indicates that black and ebony are genes at independent loci. It is likely that bronze-ebony beetles are ebony in appearance, and that black-ebony beetles are black in appearance. On these assumptions, one would expect the colors to appear in the proportions: 3 red: 6 bronze: 3 ebony: 4 black. The observations differ from this theory with a value of Chi-square of 7.00, and $0.10 > P > 0.05$ (3 d.f.). If we again suppose

black beetles to have a lower viability than normal, the results are reasonably good.

If *per contra* we assume that bronze-ebony beetles are indistinguishable from black, rather than from ebony, the expected ratios would be 3 red : 6 bronze : 1 ebony : 6 black, and the probability that the observed values represent this set of ratios is much less than 0.001 (Chi-square = 59.9, with 3 d.f.). The moderately large number of ebony individuals observed strongly suggests the first interpretation.

A further test of the independence of black and ebony is made by crossing the progeny of black x ebony back to the ebony stock. Several such crosses totalled 51 red, 45 bronze and 68 ebony. If the assumption is correct that bronze-ebony is indistinguishable from ebony, the expected ratio would be 1:1:2. The criterion of linkage is the number of red beetles compared with the number of bronze. If these are about equal, black and ebony are probably not linked on the same chromosome. If there is some linkage, the number of red will be much less than the number of bronze. The occurrence of more red than bronze indicates that there can be little or no linkage between the two gene loci.

It will be noted that in the two crosses described immediately above, the number of ebony beetles is below the number expected. A similar deficiency, but of a smaller order of magnitude, has been described by Park, Ginsberg and Horowitz (1945). This deviation from expected values does not vitiate the conclusions drawn drawn from the experiments.

Because bronze beetles are much closer in color to red than they are to black, and because the caudal cerci of bronze pupae are indistinguishable from those of red pupae, black should be described as essentially a recessive character. On this basis, McGill Black may be symbolised by *bb*, bronze by *Bb* and the normal reddish-brown color by *BB*. It might be objected that it would be better to call red *"RR"*, but as there are other mutations possible, this could be done only once. It seems better to connect the symbols with the particular mutation.

Apart from the above genetic differences, there are others which anyone handling the beetles will notice. The odor of the normal reddish-brown insects, produced by a volatile ethylquinone (Alexander and Barton 1943), is not really unpleasant. It is difficult to describe, but to J.S. at least, it is reminiscent of dilute iodine vapor, but less "clean" smelling, and a little heavier and perhaps cloying. The odor of McGill Black is easier to describe, being definitely ammoniacal in flavour (though it may contain no ammonia), somewhat putrid, and quite unpleasant. If one opens a pair of cabinets containing mass cultures of the two strains, the difference in odor is immediately apparent. A cabinet in which "reds" have been housed without much ventilation is not too smelly, whereas one housing "blacks," and long kept closed, can become really nasty-smelling. The writers are aware that the appreciation of odors is highly subjective, and the above is the best they can do in the way of descriptions.

No statistics are available, but it is the impression of J.S. that McGill Black beetles will be found more frequently *in copula* when examined in large numbers in petri dishes. Further, beginning in the third instar, and sometimes in the second, the larvae of the two mutations or strains are easily distinguishable. Those of McGill Red have tawny brown tergites, while those of McGill Black are a dusky dun color. The older punae are similar distinguishable, but the eggs appear to be identical in appearance.

It is clear that the single gene alteration leading to McGill Black has had some quite profound effects upon internal biochemistry and even upon "temperament," if we may use an anthropomorphic term. It has also altered rate of development, rather curiously, only very slightly, as will be seen later. Under the conditions of these present experiments, McGill Black is very slightly slower in its development than McGill Red, but it is not impossible that some set of conditions may yet be found under which it will develop a little faster than McGill Red. The Environmental Indices for the two should be interesting, when we have enough data to determine them (Stanley 1946).

It is suggested that inasmuch as McGill Black is almost identical in life history with the normal reddish-brown insects, it could be used as a sort of "tracer" in some experiments. When testing the egg-eating capacity of female "red" for example, the eggs found after an interval are a mixture of those left from the set put in at the start, with those laid since. If the original eggs are "black," and one presumes they are equally palatable as compared with "red" eggs, the residual eggs could be reared, and the two kinds separated on the basis of the colors of the young larvae. Inasmuch as a similar mutation is available in *T. castaneum*, again assuming equal palatability, there are altogether 4 kinds of eggs available for this sort of study.[3]

[3] Stocks of the four are available to any *bona fide* worker who wishes to have them for research. No charge is made, other than the cost of packing and air-freight, and no restrictions of any sort are imposed on the sort of work which may be done with the material.

Life Histories

Table III shows the transformation points (determined by LD_{50} analysis) for the 5 life-histories, together with their Standard Errors. The values for Combined Red and Combined Black were calculated by pooling the data and re-calculating the LD_{50}'s, as it is not legitimate to average either LD_{50}'s or their Standard Errors. It will be noted that the 5 life-histories are almost monotonously alike. In point of fact, the differences between them can only be wrung from the data by statistical analysis. Had the sampling intervals been longer, the small differences would have been completely masked.

TABLE III. *Transformation times, in hours, for the life histories discussed*

Trans. time	Red-1	Red-2	Red-3	Black-1	Black-2	Comb. Red	Comb. Black
E-1	116.86* ± 0.87	115.31 ± 1.47	116.33 ± 1.20	116.67 ± 1.29	118.01 ± 1.63	116.31 ± 0.63	117.70 ± 1.02
1-2	146.84 ± 1.05	150.86 ± 1.25	152.51 ± 1.39	150.49 ± 0.98	150.84 ± 3.05	148.83 ± 0.74	150.68 ± 1.41
2-3	224.85 ± 0.79	222.70 ± 1.52	220.08 ± 1.48	222.92 ± 2.00	221.90 ± 2.08	222.98 ± 0.93	222.41 ± 1.12
3-4	285.56 ± 1.28	281.23 ± 1.92	280.70 ± 1.63	286.42 ± 2.04	286.17 ± 2.41	283.47 ± 1.04	286.29 ± 1.26
4-5	345.24 ± 1.19	342.33 ± 2.34	343.00 ± 2.36	347.59 ± 1.89	351.01 ± 2.12	344.30 ± 0.99	347.59 ± 1.61
5-6	410.15 ± 0.81	410.18 ± 1.36	413.36 ± 1.77	418.98 ± 2.06	420.84 ± 2.15	410.98 ± 0.74	420.60 ± 1.33
6-P†	527.56 ± 2.24	538.72 ± 1.84	531.39 ± 1.41	546.70 ± 2.70	544.68 ± 2.54	534.68 ± 1.75	545.76 ± 1.66
P-A	681.51 ± 1.62	688.91 ± 2.98	679.24 ± 1.48	703.73 ± 3.71	701.41 ± 2.46	683.20 ± 1.33	702.31 ± 1.67

*No extraordinary accuracy is implied by the retention of two places of decimals. They are retained to preserve the identity of values, to make it possible to obtain differences between values, and for the convenience of those who may wish to use the values for other purposes. Observing the Standard Errors, readers may round off to suit their own purposes.

†See footnote to Table I.

Table IV shows an analysis of the differences between the various histories. The Standard Error of the differences was calculated by the usual method, assuming no correlation between members of a pair. It will be noted that, with the exception of the pair (Red-1—Red-3), the differences are not significant in the early stages, but tend to become more so as the life histories drift apart with the passage of time. An attempt has been made to show this in Figure 1, plotted from the data of Table IV, with the vertical scale exaggerated by a factor of 10. Significant differences are shown as solid circles, non-significant by open circles. In every case in which a "black" is compared with a "red," the line of the plot of Figure 1 slopes generally upward, showing that McGill Black develops a little more slowly than McGill Red. These differences may appear to the eye to be quite marked in Figure 1, but in Figure 2, where the *least* similar pair (Combined Red and Combined Black) are contrasted, it is seen that the differences are actually almost minute, though they are nevertheless real. In Figure 2, the value for each transformation point of Combined Black is plotted as an ordinate against the homologous value for Combined Red. Had the two life-histories been identical, the plotted points would lie on a straight line of slope 45°. Assuming the fitted line (dotted) to go through the origin, the slope, calculated by the method of least squares is 45° 34′, showing McGill Black to be very slightly slower than McGill Red.

It was stated in Stanley (1953b) that the value of 146 hr. for the point (1-2) in Red-1 is prob-

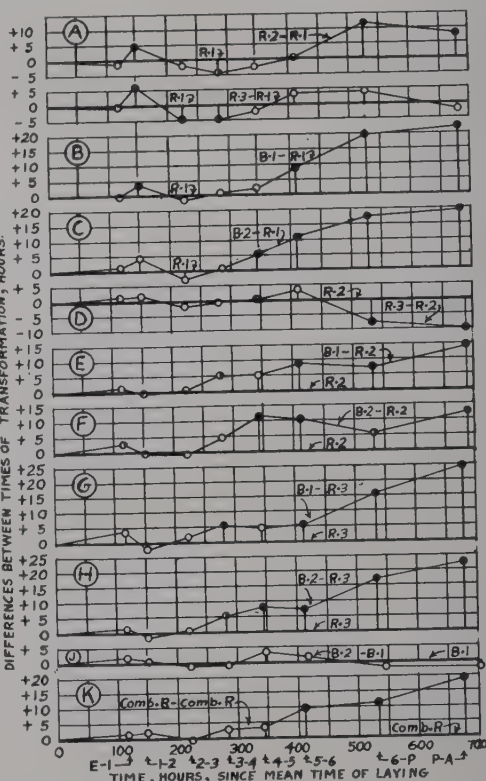


FIG. 1. Plots of the differences between the values of the 50% transformation points for successive pairs of life histories. In each diagram, the ordinate is the difference between the first-mentioned and second-mentioned, plotted against the second-mentioned, *i.e.* in Fig. 1A, the ordinate is (Red-2 minus Red-1) plotted against Red-1. Solid circles are significant differences, open circles are non-significant. Half-solid are nearly significant.

TABLE IV. *Significance of the differences between the transformation time for the life histories discussed*

Trans time, hrs.	diff, hrs.	S. E. diff, hrs.	diff / S. E.	Sig?
Red-2 *versus* RED-1				
E-1	*−1.55	±2.40	0.64	no
1-2	+4.02	±1.63	2.46	yes
2-3	−2.15	±2.93	0.73	no
3-4	−4.33	±2.31	1.87	near
4-5	−2.91	±2.62	1.11	no
5-6	+0.03	±1.58	0.01	no
6-P†	+11.16	±3.07	3.64	yes
P-A	+7.40	±3.39	2.18	yes
Red-3 *versus* RED-1				
E-1	−0.33	±2.18	0.15	no
1-2	+5.67	±1.82	3.11	yes
2-3	−4.77	±1.68	2.84	yes.
3-4	−4.86	±2.07	2.35	yes
4-5	−2.24	±2.15	1.04	no
5-6	+3.21	±1.95	1.65	no
6-P†	+3.75	±2.59	1.45	no
P-A	−2.29	±2.19	1.05	no
Black-1 *versus* RED-1				
E-1	−0.19	±2.25	0.08	no
1-2	+3.65	±1.47	2.48	yes
2-3	−1.93	±2.15	0.90	no
3-4	+0.86	±2.41	0.36	no
4-5	+2.35	±2.23	1.05	no
5-6	+8.83	±2.23	3.96	yes
6-P†	+19.14	±3.10	6.17	yes
P-A	+22.22	±4.05	5.48	yes
Black-2 *versus* RED-1				
E-1	+1.15	±2.53	0.45	no
1-2	+4.00	±3.22	1.24	no
2-3	−2.95	±2.22	1.33	no
3-4	+0.51	±2.73	0.19	no
4-5	+5.77	±2.43	2.37	yes
5-6	+10.69	±2.47	4.33	yes
6-P†	+17.12	±3.39	5.05	yes
P-A	+19.20	±2.94	6.77	yes
Black-2 *versus* RED-3				
E-1	+1.68	±2.73	0.62	no
1-2	−1.67	±3.35	0.50	no
2-3	+0.82	±2.55	0.32	no
3-4	+5.37	±2.91	1.85	near
4-5	+8.01	±2.79	2.87	yes
5-6	+7.48	±2.93	2.55	yes
6-P†	+12.29	±2.85	4.31	yes
P-A	+22.17	±2.87	7.72	yes
Black-2 *versus* BLACK-1				
E-1	+1.34	±2.78	0.48	no
1-2	+0.35	±3.16	0.11	no
2-3	−1.02	±2.89	0.35	no
3-4	−0.36	±3.23	0.11	no
4-5	+3.42	±2.84	1.20	no
5-6	+1.86	±3.11	0.60	no
6-P†	−2.02	±3.32	0.61	no
P-A	−2.32	±4.45	0.52	no

Trans time, hrs.	diff, hrs.	S. E. diff, hrs.	diff / S. E.	Sig?
Red-3 *versus* RED-2				
E-1	+1.02	±2.60	0.39	no
1-2	+1.65	±1.87	0.88	no
2-3	−1.62	±2.12	0.76	no
3-4	−0.53	±2.52	0.21	no
4-5	+0.67	±2.95	0.23	no
5-6	+3.18	±2.23	1.43	no
6-P†	−7.33	±2.25	3.26	yes
P-A	−9.67	±3.33	2.90	yes
Black-1 *versus* RED-2				
E-1	+1.36	±2.66	0.51	no
1-2	−0.37	±1.59	0.24	no
2-3	+0.22	±2.51	0.09	no
3-4	+5.19	±2.80	1.85	near
4-5	+5.26	±3.00	1.75	no
5-6	+8.80	±2.46	3.58	yes
6-P†	+7.98	±2.82	2.83	yes
P-A	+14.82	±4.75	3.12	yes
Black-2 *versus* RED-2				
E-1	+2.70	±2.90	0.93	no
1-2	−0.02	±3.29	0.006	no
2-3	−0.80	±2.58	0.31	no
3-4	+4.84	±3.09	1.57	no
4-5	+11.32	±3.16	3.58	yes
5-6	+10.66	±2.33	4.57	yes
6-P†	+5.96	±3.13	1.90	near
P-A	+12.50	±3.86	3.24	yes
Black-1 *versus* RED-3				
E-1	+0.34	±2.49	0.14	no
1-2	−2.02	±1.70	1.19	no
2-3	+1.84	±2.49	0.73	no
3-4	+5.72	±2.61	2.19	yes
4-5	+4.59	±2.60	1.77	no
5-6	+5.62	±2.71	2.07	yes
6-P†	+15.31	±2.51	6.10	yes
P-A	+24.49	±3.99	6.14	yes
Combined Black *versus* Combined RED				
E-1	+1.39	±1.19	1.75	no
1-2	+1.85	±1.59	1.16	no
2-3	−0.57	±1.44	0.37	no
3-4	+2.82	±1.63	1.73	no
4-5	+3.29	±1.89	1.74	no
5-6	+9.62	±1.24	7.75	yes
6-P†	+11.08	±2.41	4.60	yes
P-A	+19.11	±2.13	8.96	yes

*The difference is the algebraic difference between LD_{50} values for the second life history minus the first, *i.e.* −1.55=115.31−116.86. The Standard Errors are from the LD_{50}'s, and those for the combined life-histories were determined by pooling the data and re-calculating the LD_{50} and its Standard Error. A difference is considered to be significant if it is more than twice its own S.E.

†See footnote to Table I.

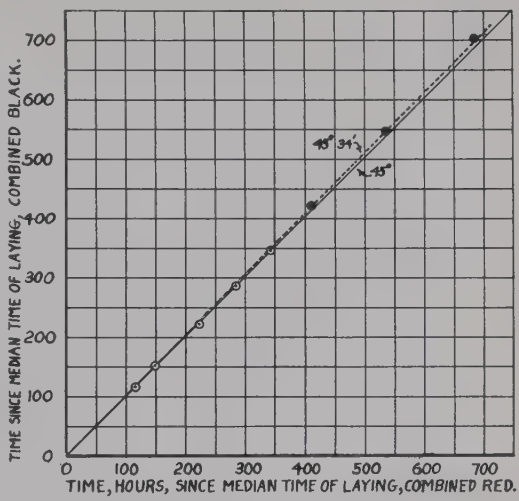


FIG. 2. The life history of "Combined Black" plotted as ordinates against that of "Combined Red." The dotted line is the least squares fit. Had the two life histories been identical, this dotted line would have lain on the solid line, at 45°. Significance of circles as in Fig. 1.

ably too low. It will be noted that it is significantly less than the homologous values for Red-2, Red-3 and Black-1. It now appears to be certain that this discrepancy is due to faulty instar-determination when Red-1 was being studied. It has subsequently been found that Dyar's Rule cannot be applied to *Tribolium confusum* (or *castaneum*) without some interesting modifications, which will form the subject of a later paper. Briefly, the head-width *decreases* during the life of a given instar, so that old specimens of say the *n*th instar become even more narrow-headed than young specimens of the (*n-1*)st instar, and can be confused with them. Our present technique is to measure every larva, and to plot the head-widths as frequency distributions for each sample. We thus obtain swarms of head-widths for each instar, and the instar of a given larva is at once determinable by noting to which swarm it belongs. Plotting time vertically, and size horizontally, the swarms are long ovals, sloping back to the left at the top, and separated by narrow sloping corridors. The top "old" end of each overlaps (to the left = smaller head) the "young" bottom end of the previous swarm. This method was just coming into use when the quadruple run of Red and Black was done, and possibly accounts for the remarkable similarity of Black-1 and Black-2. We are also studying the whole question of the relative growth of *Tribolium* heads, using autotrephon-timed samples.

In an attempt to provide some measure of the over-all degree of dissimilarity between pairs of life histories, three approximate criteria are shown in Table V. In Column 4 there appears simply the number of significant differences between pairs,

the plus sign (+) indicating the inclusion of a "nearly significant difference." In Column 2 is shown the arithmetic total (neglecting signs) of the amounts of the significant differences, each weighted by multiplying by a factor. Inasmuch as one assesses the degree of significance of a difference by noting the ratio of the difference to its own Standard Error, this ratio is used as the weighting factor in each case. In Column 3 is shown the algebraic total of the weighted differences. The criterion of Column 2 expresses the total degree of dissimilarity, while that of Column 3 gives some indication of retardation or acceleration of one member of a pair with respect to the other. It will be seen that there is general agreement between the 3 criteria in the matter of "order of merit" with respect to the degree of dissimilarity. Combined Red and Combined Black are least like each other, while Black-1 and Black-2 are most similar. Among the "reds," Red-1 and Red-3 are most alike. This is probably coincidental, as one would expect Red-2 and Red-3, reared together, to be more alike. It is again apparent that the blacks are slower in development than the reds.

TABLE V. *Weighted indices expressive of the degree of dissimilarity between the various life histories discussed*

Life-histories compared	Arithmetic total of weighted differences between transformation times	Algebraic total of weighted differences between transformation times	Number of significant differences in life-histories
Red-2 vs Red-1.....	84.8*	+ 52.8*	3+
Red-3 vs Red-1.....	58.1	− 1.4	3
Black-1 vs Red-1....	288.4	+284.9	4
Black-2 vs Red-1....	285.9	+201.2	4
Red-3 vs Red-2.....	59.8	− 46.7	2
Black-1 vs Red-2....	119.9	+119.8	3+
Black-2 vs Red-2....	151.4	+150.9	3+
Black-1 vs Red-3....	274.2	+275.0	4
Black-2 vs Red-3....	279.0	+277.3	4+
Black-1 vs Black-2...	8.7	+ 3.1	0
Comb. Black vs Comb. Red.....	312.1	+311.7	3

*See the text for the method of calculation.

One may approach the problem of the differences between life histories in another way, *i.e.* by examining the time spent, in hours, in each life-history stage. These were calculated by simple subtraction, the Standard Error of the time-span being the square root of the sum of the squares of the Standard Errors of the two ends of the interval. The results are shown for all 5 life-histories in Table VI. In the case of the time spent in the egg, the beginning of the interval is, as explained before, 0.00 ± 0.5 hr.

TABLE VI. *Durations of the life-history stages, in hours, for the life histories discussed*

Stage	Red-1	Red-2	Red-3	Black-1	Black-2	Comb. Red	Comb. Black
Eggs	116.86 ±1.00*	115.31 ±1.55	116.33 ±1.30	116.67 ±1.38	118.01 ±1.70	116.31 ±0.80	117.70 ±1.14
Larvae-1	29.98 ±1.36	35.55 ±1.93	36.18 ±2.19	33.82 ±2.04	32.83 ±3.72	32.52 ±0.97	32.98 ±1.74
Larvae-2	78.01 ±1.72	71.84 ±1.97	67.57 ±2.03	72.43 ±2.23	71.06 ±3.69	74.15 ±1.19	71.73 ±1.80
Larvae-3	60.71 ±1.50	58.53 ±2.45	60.62 ±2.20	63.50 ±2.86	64.27 ±3.18	60.49 ±1.40	63.88 ±1.69
Larvae-4	59.68 ±1.75	61.10 ±3.03	62.30 ±2.42	61.17 ±2.78	64.84 ±3.21	60.83 ±1.43	61.30 ±2.04
Larvae-5	64.91 ±1.44	67.85 ±2.71	70.36 ±2.52	71.39 ±2.79	69.83 ±3.15	66.68 ±1.23	73.01 ±2.09
Larvae-6†	117.41 ±2.38	128.54 ±2.29	118.03 ±2.19	127.72 ±2.97	123.84 ±3.45	123.70 ±1.90	125.16 ±2.13
Pupae	153.95 ±2.76	150.19 ±3.50	147.85 ±1.97	157.03 ±4.28	156.73 ±3.54	148.52 ±2.20	156.55 ±2.35

*Standard Error.
†A few 7th and a very few 8th instars are present. This is really a mean duration for the last larvae.

The values of Table VI do not yield as clear a picture of the life histories as do the transformation points and, in view of the necessity for economy of space, we deal in detail only with the differences between Combined Red and Combined Black. Table VII shows these data, whence it will again be seen that there is a general tendency for McGill Black to develop a little more slowly than McGill Red. However, the precision of the method is not sufficient to make many of the differences significant.

TABLE VII. *Significance of the differences between the durations of the various life-history stages for Combined Black and Combined Red*

Stage	Diff. hrs.	S.E. diff. hrs.	$\frac{\text{diff}}{\text{S.E.}}$	Sig?
Eggs.....	+1.39	±1.39	1.00	no
Larvae-1....	+0.46	±1.99	0.23	no
Larvae-2....	−2.42	±2.16	1.12	no
Larvae-3....	+3.39	±2.19	1.55	no
Larvae-4....	+0.47	±2.49	0.19	no
Larvae-5....	+6.33	±2.42	2.61	yes
Larvae-6*...	+1.46	±2.85	0.51	no
Pupae.....	+8.03	±3.22	2.49	yes

*See footnote to Table VI.

It would seem reasonable to conclude, on the basis of the above data and discussion, that the development of McGill Black *Tribolium confusum* is very slightly slower than that of McGill Red *confusum* at 30°C and 75% R.H. in whole wheat flour plus 3% of wheat germ. This difference

may not be apparent, or may be reversed, possibly, under other conditions. This small difference between two strains of one species is perhaps less interesting than is the fact that it could be demonstrated. It seems probable that there are many other such small differences between mutations, strains, races, etc., which might be brought out by similar experiments. Obviously, most interesting results could be obtained from studies of growth in synthetic media, with a view to assessing the importance of amino-acids etc. Combining this with the concept of the Environmental Index one might be able to make very clear assessments of the essentiality of such acids to growth and development.

We have not as yet attempted to use the autotrephen for anything but stored-products insects, but it could be used for any kind of culture for which the sample-vials do not need a frequent change of medium, provided that cooling will stop the growth.

Comparison of Autotrephon Accuracy with that of a Clock

Inasmuch as the autotrephon method is new, and has been subjected to some rather stringent criticism, it is though that it would be of interest to compare the measurement of time points with it to the measurement of time by a high-grade but moderate-priced clock, such as the ordinary person would use. Obviously a competition with a chronometer is futile. That is to say, we propose to compare the accuracy of determination of an LD_{50} point with that of a single reading of time from a clock.

With this in mind, the Western Clock Company Ltd., Peterborough, Ontario, Canada, was consulted, and they very kindly offered to perform the following experiment.

Twenty-five standard "Big Ben Loud Alarm" clocks were taken from the production line at random, and passed to the adjustment section for the standard adjustment of going-rate, made prior to distribution to the trade. These clocks were then all wound up at the same time and placed together in one room. They were wound daily, but no further adjustments were made to either going-rate or time shown. They were allowed to run in this way for 20 days, or 480 hr. The times then indicated by the clocks were converted to elapsed time for each clock, and these are tabulated in Table VIII.

It will be noted from Table VIII that the going-rates (as symbolised by the elapsed times) are fairly representative of the usual sort of random (Gaussian) distribution, complete with the usual aberrant reading, *i.e.* Clock No. 12 which ran 121 min. slow in 480 hr. Including Clock No. 12, the mean measurement of 480 hr., is 479.97 hr. with a Standard Deviation of .539 hr., and a Standard Error of ± 0.108 hr. Excluding Clock No. 12, we have 480.060 hr., Standard Deviation ± 0.362 hr., Standard Error ± 0.072 hr. Let us avoid any discrimination against the clocks, and exclude Clock No. 12.

Now the Standard Deviaton of ± 0.362 hr. is a measure of the scattering about the mean of clocks of this sort (assuming all clocks are like the 24 we used). The Standard Error of ± 0.072 hr. is a measure of the accuracy with which, using 24 clocks, we could measure 480 hr. If we had used more clocks, the Standard Error would of course have decreased, but the Standard Deviation, being a measure of the dispersion of the distribution of elapsed time (or of going-rates) would remain the same. If a single clock is taken, the measure of the likelihood that it will have a given going rate of 480 hours in 480 hours is the Standard Deviation (± 0.362 hr.) which we have deter-

TABLE VIII. *Data* from the running of 25 "Big Ben Loud Alarm" clocks, the rates of which were adjusted in the standard manner by the Western Clock Company. The clocks were then run without subsequent change of rate or time shown, for 480 hr.*

Clock No.	Final error, minutes	Clock's measure of 480 hr.
1	− 8.0	479.8667
2	−24.5	479.5917
3	−30.0	479.5000
4	+29.0	480.4833
5	−24.0	479.6000
6	+13.0	480.2167
7	+ 0.5	480.0083
8	−26.0	479.5667
9	0.0	480.0000
10	− 1.0	479.9833
11	+28.0	480.4667
12	−121.0	477.9843
13	− 1.5	479.9750
14	0.0	480.0000
15	+10.0	480.1667
16	+21.0	480.3500
17	+44.0	480.7333
18	− 3.5	479.9417
19	−13.5	479.7750
20	+41.5	480.6917
21	+50.0	480.8333
22	− 6.5	479.8917
23	− 2.5	479.9583
24	−10.0	479.1607
25	+ 0.5	480.0833

Including Clock No. 12, Mean = 479.97, S.D. = ±0.539, S.E. = ±0.108 hr.
Without Clock No. 12, Mean = 480.060, S.D. = ±0.362, S.E. = ±0.072 hr.

*The data of this Table are available through the kindness of, and by permission of the Western Clock Company, Limited, Peterborough, Ontario, Canada, makers of "Big Ben Loud Alarm" clocks.

mined. As we have only one clock, this will also be the Standard Error for this one clock.

The Standard Error of an LD_{50} is a measure of the accuracy with which the autotrephon can measure a time interval (really the combination or system of insects growing in an autotrephon, and treated as we treat them). We have to compare then the value ± 0.362 with the Standard Errors of some LD_{50}'s. Table III shows Standard Errors of the order of ± 1.00 to 2.00 hr., in 700 hr. For Combined Red, the point (5-6) is 410.98 ± 0.74 hr. This is an accuracy about half that of our hypothetical clock, so that to get the same accuracy with the autotrephon, remembering that the Combined Red value comes from 3 sub-runs, we would need 12 sub-runs with 25 insects in each vial. Inasmuch as these can be done in 3 runs using linked tracking in 4's, it will be seen that the autotrephon, while not as good as a "Big Ben" alarm clock, is not at all bad, as a time-keeper. Actually, it is vastly better than some of the early efforts of the clock industry, and probably quite as good as the average household clock with its works lubricated with a mixture of dust and kitchen vapors!

If samplng were to be at smaller intervals then every 10 hr., the autotrephon accuracy could be increased, but in view of the large effort involved in every 10-hour sampling, it is not intended to shorten the interval except in some special cases. It might be pointed out that one of the principal advantages of the autotrephon is that it allows the experimenter to escape from the "tyranny of the clock." *Any* program desired can be carried out with only occasional visits to load the controller and, if a personal note may be here interjected, J.S. still likes to look out at 2 A.M. on some of our famous Montreal blizzards, and think of the samples rolling out.

Summary

With reference to *Tribolium confusum* Duval, living in whole wheat flour plus 3% of ground wheat germ, at 30° ± 0.05°C. and 75 ± 1% (or less) relative humidity, the genetics and life history of a black mutation (McGill Black) are compared with similar information for the normal reddish-brown strain (McGill Red).

It is shown that McGill Black (*bb*) is a semi-dominant character, produced by a single gene not on the same chromosome as the single gene producing the mutation "ebony" of Park, Ginsberg and Horowitz (1945). There is also no sex-linkage.

Intermediate forms are bronze in color (*Bb*). Various crosses with ebony forms are described.

McGill Black is blacker than ebony, and can be distinguished from it by color. Larval instars and pupae can be distinguished from those of "red" insects, and it is suggested that McGill Black might be useful as a "tracer" in some studies, as apart from color, it seems almost identical with the normal reddish-brown form.

The odor is ammoniacal, putrid and somewhat offensive, quite different to the rather "clean" smell of ordinary *T. confusum*.

McGill Black develops a little more slowly than McGill Red at 30°C., but the differences are very slight, and can only be proven statistically. These differences could conceivably be reversed or eliminated under the other conditions.

A comparison is made between the accuracy of time-measurement with the autotrephon, and that of a high-grade but inexpensive alarm clock. The accuracy is about one-half that of the clock, but probably about as good as that of the ordinary worn clock. By accuracy of the autotrephon is meant the accuracy with which it will yield 50% transformation points from one life-history stage to the next.

Acknowledgments

The authors are indebted to the National Research Council of Canada for financial support of the autotrephon program. Without this support the laboratory could not be operated.

They are also indebted to Mr. J. H. Vernor, General Manager of the Western Clock Co. Ltd., Peterborough, Ontario, who authorized and supervised the trial of the clocks, and to Miss Helen J. Martin and Miss Sally Wilson, Research Assistants, who faithfully carried out the laborious examination of the samples.

They are particularly appreciative of the kindness of Dr. Thomas Park, of the University of Chicago, who provided the subculture of the mutation "ebony."

Mr. J. W. Pollock, Instrument Maker to the Department of Zoology at McGill University, who made most of the autotrephon, continued to function as the man who answered the anguished calls for help. The authors are *more* than grateful to *him!*

References

Alexander, P. and D. H. R. Barton. 1943. The excretion of ethylquinone by the flour beetle. Biochem. Journ., **37**: 463-465.

Bliss, C. I. 1935a. The calculation of the dosage-mortality curve. Ann. App. Biol., **22**: 134-167.

———. 1935b. The comparison of dosage-mortality data. Ann. App. Biol., **22**: 307-333.

Brindley, T. A. 1930. The growth and development of *Ephestia kuhniella* and *Tribolium confusum* under controlled conditions of temperature and relative humidity. Ann. Ent. Soc. Amer., **23**: 741-757.

Chapman, R. N. and Lilian Baird. 1934. The biotic constants of *Tribolium confusum* Duval. J. Exp. Zool., **68**: 293-305.

Dyar, H. G. 1890. The number of moults of lepidopterous larvae. Psyche, **5**: 420-422.

Mather, K. 1947. Statistical analysis in biology. New York: Interscience Pub., 2nd ed., 267 pp.

Park, T., B. Ginsberg, and S. Horowitz. 1945. Ebony: a gene affecting body color and fecundity of *Tribolium confusum* Duval. Physiol. Zool., **18**: 35-52.

Reynolds, J. M. 1945. On the inheritance of food effects in a flour beetle, *Tribolium destructor*. Proc. Roy. Soc. London, (B) **132**: 438-351.

Stanley, J. 1939. Time required for the development of *Tribolium* eggs at 27°C. Ann. Ent. Soc. Amer., **32**: 564-568.

———. 1951. The autotrephon: an apparatus for rearing insects under controlled conditions with automatic time-controlled withdrawal of samples. Ecology, **32**: 413-442.

———. 1953a. Studies from the autotrephon, I. Some points in general operation and maintenance. Ecology, **34**: 21-28.

———. 1953b. Studies from the autotrephon, II. The analysis of autotrephon data. Ecology, **34**: 29-43.

Sweetman, M. D. and L. S. Palmer. 1928. Insects as test animals in vitamin research, I. Vitamin requirements of the flour beetle, *Tribolium confusum* Duval. J. Biol. Chem., **77**: 35-52.

TESTING THE LINE-STRIP METHOD AGAINST FULL TALLIES IN DIVERSE FOREST TYPES

Alton A. Lindsey
Department of Biological Sciences, Purdue University, Lafayette, Indiana

Introduction

The line-strip method was developed during a phytosociological study (Woodin and Lindsey 1954) of an association characterized by unusual simplicity of tree species composition, the juniper-pinyon woodland. The species-area curve is obviously unsuited for use where few species occur. Even though a very small aggregate sample were to include all the species, there would be an extremely low probability that the areas sampled would adequately represent the station with respect to the coverage, density, frequency, and other attributes of these species. Whether a stand includes a small or large number of significant species, a much better criterion of sampling adequacy (than the inclusion of an increasing number of progressively less important species) is based on the standard errors of the important attributes of the dominant and other well-represented species.

Several points important to the line-strip method have been brought out in recent phytosociological literature: (1) the importance of cover as an expression of dominance, (2) the value of the line-interception principle for measuring crown cover, (3) the variability inherent even in quite randomly dispersed populations (Cottom, *et al.* 1953), (4) the superiority of long, narrow, rectangular quadrats for reducing the variance among plots (Bormann 1953), (5) the need for very thorough sampling for the often clustered dispersal type in natural populations, (6) the advantage of rapid, mechanically simplified field techniques to make such sampling feasible, and (7) application of statistical methods to demonstrate sampling adequacy.

In using the line-strip sampling unit, coverage is taken from crown interceptions on a long, randomly placed line, surveyed by steel tape, while density and frequency are derived from an unsurveyed strip of equal length and extending ten feet to each side of the line.. The combination of linear and areal methods is used because the quadrat method is unsuited for direct cover determinations, while the line alone is unsuited to anything else, giving biased estimates of density, frequency, and basal area because the larger species have greater probability of being sampled. After it proved satisfactory in juniper-pinyon in 1951-53, the writer modified the method for use in stands of tall conifers, and, possibly, deciduous stands. This paper reports the testing of this sampling technique by statistical analysis and by comparison with full counts in stands of four forest types. The field work was done during the summer of 1953.

State forestry officials in Michigan were helpful in locating old growth stands in the jack pine plains, and in suggesting the little-known red and white pine forest, which is one of only two such virgin stands in the Lower Peninsula. Dr. W. K. W. Baldwin of the National Museum of Canada, the authority on Ontario flora, recommended the Chain-of-Lakes spruce-fir stand as most representative, and Mr. Ed Bonner, forester of the Spruce Falls Power and Paper Company aided in selecting a specific station site and arranged accommodations in a lumber camp of this firm. Prof. W. C. Allee kindly permitted the study of an almost undisturbed portion of his maple-beech forest near Annapolis, Indiana. David E.

Lindsey assisted in the field. The Purdue Statistical Laboratory made the standard error determinations; Dr. Virgil Anderson and Mr. Joseph Navarro of this laboratory gave statistical advice and critically read the manuscript. A Sigma Xi-Resa grant-in-aid in gratefully acknowledged. Nomenclature used is that of Gleason (1952).

Methods

In the formulae given below for certain phytosociological concepts, analogous features are brought out by corresponding subscript numbers.

The terms refer to a given station, to the two main size classes (above and below 4 in. d.b.h.) separately, and to sampling units of equal size and type for a particular set of observations. N may represent the number of individuals of a given species in all areal plots, N_t the total number of individuals of all species in all areal plots, n the number of areal plots (either whole strips or strip-section quadrats), n_s the number of areal plots in which a given species occurs, n′ the number of lines used, and a is the area of one of the areal plots in square feet. In these terms, the various expressions of density are: density per square foot $D_o = N/na$, mean strip density (or mean strip-quadrat density) $D_1 = N/n$, density per acre $D_2 = D_o$ (43,560), relative density or per cent total abundance $D_3 = 100\ N/N_t$, and mean area per individual (Curtis and McIntosh 1950) $M = 1/D_o$. Based on numerous strip-quadrats, frequency $F_1 = 100\ n_s/n$, and relative frequency $F_3 = 100\ F_1/F_t$ where F_t is the total of frequencies for all species. Also based on strip-quadrats, mean plot abundance $A_1 = N/n_s = 100\ D_1/F_1$. Neither abundance in this sense, mean area, nor frequency values are necessarily employed in the line-strip method.

The expressions of trunk basal area at 4.5 ft. are mean basal area per strip (B_1), square feet basal area per acre (B_2), and relative basal area (B_3) or 100 times the sum of basal areas for one species in all strips, divided by the total basal area of all species in all strips.

Only the various crown cover expressions are derived from the line. Let I represent the sum of interception distances for a given species on all lines, I_t the total interception distance for all species on all lines, and L_t the total length of all lines collectively. For the standard line length used, mean line cover $C_1 = I/n'$, square feet cover per acre $C_2 = C_4$ (43,560), relative cover or per cent vegetation cover $C_3 = 100\ I/I_t$, and per cent ground cover $C_4 = 100\ I/L_t$.

Woodin and Lindsey (1954) utilized a special form of line-strip, the elb (an L-shaped unit having arms of equal length) because strong influence of substrate and microtopography in the juniper-pinyon region is often expressed in a linear way, producing vegetational bands and alternes. Random placement of straight line-strips, or placing them so as to cut across contours, would appear to yield less representative sampling over such terrain than random placement of the same number of elbs. On the average, the elb form includes more of the minor variations within a given sampling unit, thus reducing the variance between different units. However, most forest types occur where the bedrock is covered more deeply and surface erosional effects are less pronounced. The advantage of the elb form in the rather uniform and level terrain of the stands tested was considered too slight to justify the inconvenience of surveying elbs, so that the straight line-strip has been used throughout the present work. This was 400 ft. long and 20 ft. wide for all the stands, and from 6 to 10 were used per station. An even greater length would be desirable if only sampling were being done; however, in comparing with full counts a longer line-strip is impracticable since it necessitates an area which is too large for counting all trees therein.

After the boundaries of the station had been surveyed and mapped on graph paper, the position and orientation of the lines were determined by a random numbers table and mapped. A Brunton compass and Jacob's staff were used in surveying the boundaries and the lines. A 200 ft. steel tape marked in feet was staked out twice for each line. For making complete counts, the station area was marked off by white cord in unsurveyed lanes about 100 feet wide. Various things were tried for marking trees as counted, including yellow "Markal" wax crayon, spray paint from pressure cans, and short lengths torn from rolls of crepe paper ribbons. The most satisfactory was simply tearing facial tissue into strips in advance, and twisting a strip over a low branch, or pressing it against the rough trunk. It is needed for only a few minutes to prevent counting a tree twice in working from side to side along the lane. For temporary markings, some workers hit the trunk with a cloth bag of lime.

For cover determinations, a sighting-level (Fig. 1, S) was designed to aid in finding line-interception points. A straight 5 ft. length of quarter-round was used; a foot from the lower end of this, on a flat side, was fastened a glass "bubble-tube" replacement for a carpenter's level, so that the bubble centered when the stick was exactly vertical. A small round-headed screw was also cen-

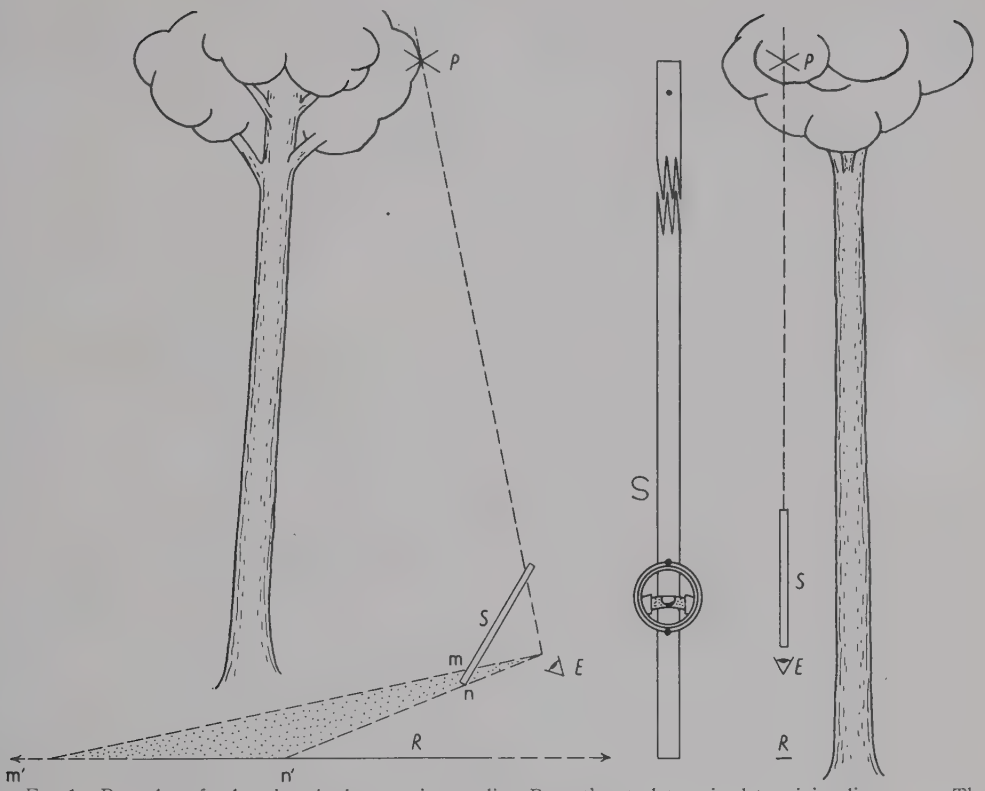


FIG. 1. Procedure for locating the interception reading R on the steel tape in determining line cover. The five-foot sighting-level (middle) is used in two positions. The same tree is shown; the plane of the right diagram is 90° from that of the left. The operation shown at left locates the crown edge point P; the figure at right shows how the tape reading (R) directly beneath P is located. A full explanation is given under "Methods."

tered on the same side but near the upper end of the stick.

The object is to locate the tape reading (Fig. 1, R) of each edge of the crown projected downward, which could be done by repeated trial and, error 90° rotation of the vertically held sighting-stick. However, the method diagrammed is easier and faster. Since R is on the line directly beneath the crown edge point P, the latter must be found first (Fig. 1, left). The operator faces along the stretched tape, holding the level at about a 45° angle in front of him and overhead so that the eye (E) lines up a portion of the lower edge (m-n) with the distant tape length (m'-n') on the vertical visual plane Emm'n'nE. Without moving the stick, he glances upward to locate the point (P) on the crown edge intersected by the upper portion of the stick. This point is directly above the line; to find the exact spot (R) along the line which it is above, the operator turns 90° to face out away from the line. This is shown on the right side of the figure, in which only a cross-section of the line appears. Aiming the now almost vertical stick (S) at the previously determined point P while the horizontal bubble tube is oriented parallel (not transverse) to the tape, he moves along the tape until the bubble is centered, then lowers the stick to point R and records the reading to the nearest foot in the first column of the field record form. This procedure is accomplished very rapidly after a little practice.[1] Line interception of trees having trunks not less than 4 in. d.b.h. is included whether or not the trunks occur inside or outside the strip.

The operator then follows along the line to a point even with the tree trunk and records in the fourth column (for all trunks 4 in. and over having centers in the strip whether or not their crowns contribute line cover) the tape reading where an imaginary side line projected to the

[1] Another type of sighting-stick has two levels mounted at right angles on the two flat sides of the quarter-round. Its use is simpler, but more tiring.

trunk center is at right angles to the tape line. The d.b.h. of such trunks is measured by a diameter tape. The interception point of the far edge of the tree crown is then determined with the sighting-level, and recorded in the second column. Substracting the first interception figure from the second, ordinarily done in the office, yields the individual's line-interception for the third column. Because of crown overlapping, it is possible for the sum of the ground cover (C_4) figures for all species to exceed 100 per cent; this is not true of the C_3 percentage, which is based on the total of interceptions rather than on the fixed line length.

Since 10 ft. can be closely estimated, the 20 ft. strip width is maintained without routine surveying. When it is questionable whether a tree-center falls within the imaginary strip boundaries, this is checked by twice laying out the 5 ft. sighting stick on the ground. The fourth column furnishes raw data for the various density (D) and basal area (B) expressions, and, based on subdivisions called "strip-quadrats," those for frequency (F) and abundance (A). The same column is used for studying the nature of dispersal from either the strip-quadrat, in the same ways as in the quadrat method, or the intervals between successive fourth column entries within the entire strip for a given species.

Stems having a d.b.h. measurement less than 4 in. were considered separately. On the right half of the field record sheet, such reproduction cover data were usually recorded from only a half or quarter of each line. In a final column, a running tally of numbers of each species within the same portion of the strip furnished reproduction density data. No line-interval measurements were taken, as was done for the mature individuals.

Although no real difficulty was encountered in the virgin deciduous stand sampled, probably interlacing branches of some deciduous forests would interfere with cover sampling. Such difficulty is considerably mitigated by the fact that when individual crowns of the same species lie adjacent over the line (as often occurs with dominants or aggregated species), the location of the boundary between them is immaterial. If an accessible stand proves difficult in summer, it could be sampled in autumn when the foliage has thinned sufficiently for adequate visibility. Crown cover studies in winter have been carried on routinely by D. DenUyl in Indiana (personal communication 1954). To make such data comparable with results from trees in leaf, a figure for cover increment due to leaves at crown edges might be worked out for each species.

Either density (D_1) or cover (C_1) data from approximately the first six line-strips run at a station may be used to estimate the final number (n) of these sample units needed there to reduce the per cent standard error to a desired level (r) in the final results. This is done by the formula

$$n = \frac{s^2 \quad 100^2}{\bar{x}^2 \, r^2}$$

where s^2 is the observed variance and $\bar{x}$ is the observed mean from the six samples taken first. The r figure used is an integer. Assuming that s^2 equals the variance of, and $\bar{x}$ equals the mean of, an infinite number of samples, there is a 67 per cent probability of obtaining a final per cent standard error as small as r or smaller. Since the estimate of n is thus a rough one, at least one line-strip more than the indicated n value should be used.

The above formula is applied to one or two species only moderately well-represented in the stand, rather than the most abundant ones. An r value not higher than 20 is suggested for such species. The estimate of n is derived from strips (density) or lines (cover); since the two are equal in number and length the n derived from either refers to line-strip units. If wide discrepancies in sampling accuracy between lines and strips are found, the strip width should be changed for subsequent sampling in the same type. This is discussed below.

The Forest Stands

To enhance the value of the complete tallies, the four stands were carefully selected for best possible representation of aboriginal conditions in associations of their type in their general region. Investigation of the human history of each stand gave no indication that cutting or other disturbance affecting the natural attributes of the tree stratum had occurred since white settlement. Data derived from the sampling method will be given in a later section; the following is general information regarding the stations selected.

Station W, Jack Pine, Crawford Co., Michigan

This stand occurs west of Pickerel Lake in the central southwestern part of Section 24, T 28 N, R 1 W, on Grayling sand. It is on State land within the Au Sable State Forest. Twenty acres were surveyed and every tree (4" d.b.h. and over) within this area recorded. Ten line-strips were used; the total strip area covered 9.19 per cent of the twenty acres. Reproduction was scanty; it was recorded for the entire length of all line-strips.

The physiognomy differs from that of the familiar second-growth jack pine (*Pinus banksiana*

Lamb.). The stand is open and the crowns low-branched and spreading. The largest trunk measured was 26 in. d.b.h. Increment cores showed the oldest trees were about 70 years. Old fire scars were noted on the southeast side of a few trees at one corner of the station. Oaks, always clustered, were stunted and atypical, since they were near their botanical range limits. The average numbers per acre of the subordinate species were: 1.5 *Quercus velutina* Lam., 1.1 *Q. palustris* Muench, 0.25 *Q. borealis* L. (?), 0.2 *Q. alba* L., and 0.1 *Pinus resinosa* Ait.

Station X, Red Pine-White Pine, Roscommon Co., Michigan

Located in the extreme northeastern corner of its county, this unusual remnant of the "lake forest" occurs in the extreme southeastern corner of Section 2, R 1 W, T 24 N. The land is State-owned, in the Ogemaw State Forest. Mr. E. B. Hollowell, who homesteaded the northern half of the same section in 1882 before any lumbering in this vicinity and has lived here ever since, accompanied the writer to select a sampling station in a portion of the approximately 20 acres of virgin timber. Red pine (*Pinus resinosa* Ait.) and white pine (*P. strobus* L.) were dominant; jack pine was abundant but scattered. The only significant hardwood was black oak.

An 11.137 acre station was fully counted. The 10 line-strips sampled covered 16.4 per cent of the station area. Reproduction records were limited to 200 ft. of the line-strip length, or a total of 2,000 ft.

The largest d.b.h. measurement for white pine was 32 in., for red pine 28.4, and for jack pine 27.

Station Y, White Spruce-Black Spruce-Balsam Fir, County of Cochrane, Ontario, Canada

Representing the boreal forest type of northern Ontario, this station was located on the restricted Chain-of-Lakes road south of Moonbeam, a village east of Kapuskasing. It is on Crown land in the northern part of the township of Castleman, lot IX, concession 1. The 8.264 acre area for the full count lies directly north of mile 7 on the road. Six line-strips comprised 13.3 per cent of the station area. Reproduction was considered for only 100 ft. of each sample unit.

Records of the Spruce Falls Power and Paper Company for this general region show a number of white spruce attaining 98 ft., and one 108 ft. 9 in. tall. They seldom exceed an age of 180 years, but "occasionally reach 200." Mr. Bonner wrote (private communication 1953), "Black spruce on well-drained sites will reach a maximum of 75 ft. (rarely 90) and a maximum age of 200 years. In the swamps and flats . . . a maximum height of 70 ft. (rarely 80) and ages up to 250 years. . . ."

The station was in the type classed by local foresters as "softwood slope, hardwoods less than 25 per cent," in contrast with "softwood flat" and "swamp" sites having poor drainage.

Station Z, Sugar Maple-Beech, Parke Co., Indiana

The 200-acre Allee Woods is in north-central Parke County, northwest of Annapolis village. The 6.24 acres surveyed lie on gently southward-sloping upland between two deep ravines tributary to Sugar Creek. The seven strips comprised 20.6 per cent of the full tallied area, which contained 20 tree species, most of them in very low density. All non-reproduction size trees average 107 per acre. Sugar maple (*Acer saccharum* Marsh.) and beech (*Fagus grandifolia* Ehrh.) together constitute 56 per cent of the total number of all (non-reproduction size) individuals; the full tally showed exactly twice as many maple as beech. Reproduction of maple was abundant but clustered. One-fourth of each line-strip was utilized for records on reproduction; because of extreme variance even the full length would not have yielded accurate data on reproduction.

The subordinate species were tulip tree (*Liriodendron tulipifera* L.), sassafras (*Sassafras albidum* (Nutt. Nees.), white oak (*Quercus alba* L.), red oak (*Q. borealis* Michx. var. *maxima* (Marsh.) Ashe, black oak (*Q. velutina* L.), and pignut hickory (*Carya glabra* (Mill.) Sweet). Those sampled too infrequently for tabulation, with their mean actual density per acre, were: 2.4 white ash (*Fraxinus americana* L.), 1.6 shagbark hickory (*Carya ovata* (Mill). K. Koch), 1.4 black walnut (*Juglans nigra* L.), 1.3 dogwood (*Cornus florida* L.), 0.6 white elm (*Ulmus americana* L.), 0.6 slippery elm (*U. rubra* Muhl.), 0.5 *Fraxinus* sp., 0.5 black gum (*Nyssa sylvatica* Marsh.), 0.3 yellow oak (*Q. muehlenbergii* Engelm.), 0.16 butternut (*Juglans cinerea* L.), and 0.16 hackberry (*Celtis occidentalis* L.). The numbers of medium-size sassafras suggest that light, scattered selective cutting had once opened the stand somewhat.

Results

Table I sumarizes the community analyses of the four stands. It includes only the non-reproduction class trees; percentage figures are calculated relative to the total population of such trees only. Definitions of column headings are given under Methods, except for index of dispersal which is discussed below.

Standard error calculations were based on fig-

TABLE I. *Phytosociological attributes, and their per cent standard errors, for four distinct communities as determined by line-strip sampling, and actual density per acre from complete counts of the same areas. For explanation of symbols see Methods sections*

Station	Species	Density per acre: Whole-strip D_2 & standard error	Density per acre: True D_2 from full tally	Relative density, D_3	Frequency F_1	Index of dispersal	Basal area B_2 (sq. ft./acre)	Relative basal area B_3	Crown cover, in % of: Veg. C_3	Crown cover, in % of: Ground C_4	Per cent standard error of mean: D_1 per strip-quadrat, alternate	Per cent standard error of mean: D_1 per whole strip	Per cent standard error of mean: Line cover C_1	Per cent standard error of mean: Basal area B_1
W														
Crawford Co., Mich.	*Pinus banksiana*	126 ±14	126	93	92	1.140	53.6	98	93	41	15	11	10	8
	Quercus spp.	.....	..	7	12	..	0.9	1.7	6.6	0.29	..	..	..	..
X														
Roscommon Co., Mich.	*Pinus resinosa*	46 ± 5	44	33	57	1.259	132	58	45	30	13	11	11	10
	P. strobus	27 ± 5	27	20	48	0.956	69	30	26	17	21	19	24	31
	P. banksiana	39 ± 7	62	28	46	1.461	18	8	12	8	24	19	23	22
	Quercus velutina	16 ± 4	28	11	26	1.245	4	2	10	7	29	27	29	33
	Others	.....	..	8	..	.....	5	2	7	4.5	..	..	..	..
Y														
Kapuskasing, Ontario	*Picea glauca*	64 ± 5	67	31	75	1.067	56	44	20	9.6	9	8	25	7
	P. mariana	41 ± 9	36	20	54	1.206	25	20	17	8.2	29	22	25	12
	Abies balsamea	61 ±12	77	29	77	0.949	15	12	22	10.7	21	19	25	20
	Betula papyrifera	32 ± 5	32	15	46	1.183	19	15	33	16.3	25	17	9.5	13
	Thuja occidentalis	9 ± 3	7	4	17	11.18	5	4	4	2.1	52	33	53	36
	Populus balsamifera	2.7 ± 1.8	3.3	1.3	4	1.531	6	4.5	4.5	2.2	..	69	100	..
Z														
Annapolis, Indiana	*Acer saccharum*	50 ± 6	40	37	68	1.003	54	38.3	40.2	50	14	13	9	44
	Fagus grandifolia	20 ± 7	20	19	38	0.971	47	33.2	31.5	39	40	37	16	39
	Liriodendron tulipifera	9.3 ± 3	10	9.5	16	1.228	13	9.2	5.7	7	31	33	31	35
	Sassafras albidum	10 ± 5	7.8	7.4	16	1.331	5.6	4.0	3.7	4.6	73	50	36	61
	Quercus alba	6.2 ± 2	7.7	7.2	12	1.118	9.5	6.8	4.1	5.0	50	34	50	77
	Q. borealis	2.3 ± 1.6	3.3	3.2	7	0.738	3.6	2.5	3.4	4.2	..	69	40	..
	Q. velutina	3.9 ± 2.6	3.0	2.9	11	0.765	2.8	2.0	4.3	5.3	69	66	74	..
	Carya glabra	5.4 ± 3	4.5	4.2	11	1.073	4.6	3.3	4.8	6.0	65	58	51	..

ures per line-strip. For example, we determined for Station W jack pine the standard error of the mean of the ten figures that show the number of individuals in each of the ten 400 x 20 ft. line-strips. This mean is the D_1 figure. In the last four columns, the ratio of the standard error to such a mean is expressed in per cent as a coefficient of variation for several different attributes. The table also shows the whole-strip sample mean and its standard error expressed on a per acre basis for D_2, but not for B_2 or C_2.

Frequency is based on stem centers occurring within 50 x 20 ft. subdivisions of the strip called "strip-quadrats," none of which were discarded for this calculation.

The full count in the entire 20-acre stand at Station W showed 2,524 jack pines present, while the estimate derived from strips was 2,515. Similar very high degrees of correspondence obtained in various other stands—for white pine, red pine, paper birch, and tulip tree. It is possible that these are chance results and that if the strips had fallen differently in the random placement these species might have shown less close, and other species closer, agreement between estimated and actual. Therefore, the standard error of the mean D_2 estimate (Table I) is required for a statistically valid comparison with the actual count of density per acre (adjacent column). In the jack pine stand, fewer sampling units than 10 would have sufficed. At Stations Y and Z, the high per cent standard errors for some of the species indicate that more units would have been desirable.

The proper width of line-strip units

If a species-by-species comparison of per cent standard errors for density *vs.* line cover were to show that either one had consistently lower errors, some width other than 20 feet might be desirable for the areal component of the sampling unit. In other words, if cover had been sampled in general much more adequately, the strip width should be increased to include more trunks for the same line-length, tending to equalize the accuracies.

Eight of the species are conifers and 11 are hardwoods. As shown in adjacent columns for per cent error, six of the conifers have the density error lower; in the other two conifers, the cover (C_1) and D_1 figures are equal or within 1 per cent of equality. Seven of the hardwoods show better sampling for cover, in two of them it is essentially

equal, and in two it is considerably better for density. On this basis alone, it would seem that the strip might be narrowed for conifer stands and widened slightly for deciduous stands of the type studied. However, experience indicates that a strip much wider than 24 feet would require actual measurement of distance away from the line for a higher proportion of trees, thus slowing the work. Reducing the width below 20 ft. is not recommended because the mechanics of sampling for density is enough easier than for cover that a slight accuracy differential favoring density may be justified. The general balance found between the density and cover errors suggests that as a standard strip-width for routine use in different forest types, 20 feet is quite practicable. If a 24 ft. width were adopted for deciduous stands, the sighting-level would be lengthened to six ft.

Sampling adequacy for basal area vs. cover

Basal area is commonly used as an expression of dominance because it is believed easier to obtain than crown cover and the two are more or less related. The direct measurement of crown cover by line interception provided a comparative basis for determining which is sampled more accurately in the line-strip method, where basal area is sampled from trees within a 20 foot areal strip of the same length as the line on which cover interception is taken. It is assumed that if either expression yields consistently lower per cent standard errors it is to be preferred, other things being equal. There are no true cover figures to check estimates against as was done for density. The last two columns of Table I provide a comparison of per cent standard errors for C_1 (line cover figures from strips) with the corresponding percentage figures for B_1 (basal area estimates from the same strips).

Jack pine at both stations of occurrence (W and X) and red pine had the two errors essentially equal, *i.e.*, within 2 per cent. The four species that had the error for line cover materially higher were all conifers and all four were at the spruce-fir (Y) station. Sampling in these species for basal area had been better than that for cover. White pine was the only conifer that showed better sampling for crown cover. Its spreading crown resembles the form occurring in deciduous trees. All deciduous species, whether in mixture with conifers or not, showed materially higher per cent errors for basal area than for line cover. This was particularly true of the dominants beech and maple.

The use of whole strips vs. alternate strip-quadrats

Bormann (1953) found that sampling alternate sections of a strip gave nearly as accurate basal area results as the whole strip. This idea was tested for density estimates with the present method and data. In each strip, counts were made from alternate strip-quadrats; four of the eight, each 50 x 20 ft., were used in each strip. Per cent standard errors for the resulting D_1 densities may be compared with whole strip D_1 errors in adjacent columns of Table I. For all but one species, the whole strip error was less than that of alternate sections. The exception, tulip tree, had a difference of only 2 per cent. Disregarding balsam poplar and red oak because their errors by alternate sampling were indeterminable, the total error per cent from alternate sampling was 122 per cent of that from whole strips, although a better comparison is that for one species at a time. From the latter, it appears that (with the exception of the jack pine at Station A and of black spruce) the dominants were sampled very nearly as well by alternate plots. The other, less abundant, species were generally sampled materially better by whole strips. To sample as well by alternate strip-quadrats as was done by the number of whole strips used, additional line-strips would be required, whereas it is much simpler field procedure to use the full length of a smaller number. When the tape is placed for alternate sections of a strip it is in position for all sections, and a density count throughout the strip is not time-consuming in view of its increased accuracy over that from alternate 50 ft. quadrats.

The nature of dispersal

The dispersal index D_1/d_1 was computed (Table I) where D_1 is the mean density per strip-quadrat, and d_1 the corresponding density expected from the known frequency (Fracker and Brischle 1944, Table I). While random is not separable from clustered dispersal by definite limits, the close approach to unity found in all dominants indicates a high degree of randomness. The only species deviating drastically (11.18) from randomness was *Thuja occidentalis*. Its clustering was evident by field observation, since it was confined to scattered wet spots at Station Y.

The methods applicable to ordinary quadrats would apply equally well to the strip-quadrat subdivisions of line-strips. In fact, they might apply better because of the wide choice of quadrat size possible later during the office phase of the study. The distances between figures for trunk centers projected to the line, for a given species, provides

another method of determining dispersal and is currently being studied in two other laboratories.

Reproduction

Reproduction-class data was incidentally obtained but is not reproduced here. The accuracy of these figures is decidedly lower than in the case of mature trees, because for three stands only a continuous half or quarter of the line-strip length was used for reproduction sampling; only for Station W was it sampled along the entire length. The variance of reproduction figures per sampling unit was high; better reproduction sampling would have been needed had the intended aim been primarily to describe the stands.

At Station X, the per cent standard errors for D_1 from half strips, for individuals less than 4 inches d.b.h., were as follows: red pine 29, white pine 26, jack pine 71, and black oak 32. Even the lowest of these is somewhat beyond the acceptable limit for satisfactory sampling.

Discussion and Conclusions

In tracing the history of techniques in general, Toynbee (1946) discerns a trend which he calls "etherialization" whereby refinements bring about reduced dependence on material factors, *e.g.*, radio and television are more etherial media than telegraph and telephone. A similar trend has occurred in the development of ecological sampling techniques. Surveying quadrats involves so much mechanical labor that workers may be unable or unwilling to use enough quadrats to demonstrate statistically that sampling is adequate for the most important attributes of even the few dominant species. The line interception method introduced by Canfield (1941), the point contact method of Levy and Madden (1933), the application of airphotos to forest type mapping, the random points method and its quadrat modification by Cottam, *et al.* (1953) offer advantages over quadratting. The variable-radius method of Bitterlich (Grosenbaugh 1952) which is "plotless" in practice but not in theory, culminates the etherialization process. The ideal result of this trend (only partially attained by any method) is to liberate workers from some of the mechanical routine during field work, thus facilitating the collection of sufficient data for statistical validation of sampling adequacy, without sacrificing desirable parameters. The newer rapid (quadrant and variable-radius) methods, were proposed for preliminary surveys and may not yield information on all the vegetational attributes required in a detailed study.

Many forest ecologists have recognized the paramount importance of crown cover but relatively few have measured it directly due to difficulties inherent in their sampling methods. Weaver and Clements (1938) wrote, "In dynamic ecology, dominance, subdominance, and subordination represent the primary numerical and process relations of component species, and serve as the proper basis for describing communities, measuring yield and reaction, and tracing changes in composition and structure." Penfound (1945) considered that "areal cover is more important than frequency or density in the study of plant communities." Workers using the quadrat method and recently developed rapid survey methods have necessarily depended upon trunk basal area for dominance estimates, since only linear methods are well adapted for crown cover measurements. Buell and Cantlon's (1950) comparison based on pine barrens trees and shrubs led them to state, "The transect (line) method is considered to yield more valuable data than the quadrat method." They pointed out the weakness of the quadrat method for measuring the open spaces between crowns and the crown cover itself.

Because the linear unit used alone gives unbiased estimates only for coverage values, Woodin and Lindsey (1954), and Niering (1953) independently, used linear and areal sampling units together. The complexity of the density formula derived by Hoel (1943) for line sampling theory shows the utter impracticability of obtaining unbiased density estimates from line interception.

Ground cover is both more significant and more accurately estimated than per cent vegetation cover. Because of uncovered ground, overlapping crowns, and the undesirability of estimating it from basal area without special correlation studies of the species involved, ground cover should be obtained in detailed studies by direct measurement of crown interception. A basal area estimate for one species expressed relative to total basal area of all species present may not give an adequate indication of vegetation (crown) cover. This is especially true in mixed conifer-hardwood stands, as attested by our data and by that of Chisman and Schumacher (1940). They reported that in pine-hardwood types of the Piedmont Plateau "pine trees over 4 inches in d.b.h. occupy very much less crown area for their sizes than the hardwood trees." A per cent vegetation cover figure, like the other subscript 3 expressions relative to the vegetation as a whole, has the marked disadvantage that the many less common species are not sampled nearly as well as the few dominant ones, thus reducing accuracy for the latter. This objection does not apply to relative ground cover (C_4), which is calculated against a base

figure uninfluenced by the quality of sampling for any species.

Although general conclusions should not be drawn from only one deciduous stand, in the maple-beech area studied, the sampling proved much better in the direct cover measurements than in those for basal area. Density sampling also gave a much lower per cent standard error than basal area sampling. Therefore, increasing the strip width enough to balance density errors with cover errors would fail to improve basal area sampling to a comparable degree. This suggests that direct cover determination is even more desirable in deciduous forests than in eastern coniferous stands where it is mechanically easier to perform.

Comparison of errors for juniper-pinyon in the data of Woodin and Lindsey (1954) shows that line-strips 20 ft. wide sampled density better than cover, but without enough difference to justify use of a narrower strip in this type. The same applies to conifers in the present study in contrast to the one hardwood stand. Judging from spruce-fir, red pine-white pine, jack-pine, and juniper-pinyon, 20 ft. gives slightly more than the minimum width needed to balance density and basal area against cover sampling in conifer stands. Twenty feet is the recommended width for these types, while 24 ft. may be tentatively suggested for deciduous stands. In a second-growth *Quercus-Acer-Ulmus* stand used in a class exercise, a 24 ft. width gave slightly better sampling for density than for cover on the line.

The importance of permanent sampling units has often been stressed. An outstanding advantage of the line-strip method lies in the ease of marking the few units for future work, in contrast to the numerous quadrats which would be required for the same aggregate sample area. Seven-foot steel fence posts having T-shaped cross sections are cut into half lengths. One such stake, conspicuously painted, is driven 1.5 ft. into the ground at each end of a line, with the stem of the T pointing down the line toward the opposite stake. A precise compass bearing may be painted on one of the stakes marking each line. The original graph paper map of the station, showing the lines, should be kept as a permanent record.

In studies including shrub and herb strata of the forest, the line for each lower stratum coincides with a portion of the longer line used for the next higher stratum. The steel tape need be stretched only once to sample all strata for cover, density, and areal frequency determinations. Boundaries of the strip, which may vary in width for different strata, need not be laid out on the ground. This permits a saving in routine labor in contrast to quadratting.

Frequency can be compared only when quadrats are of equal area. On the basis of the line-strip field record sheets, comparison with the results of other workers may be made at any time by selecting a strip-quadrat length to yield the same area as used in other studies. For the primary computations, a convenient strip-quadrat size is 50 by 20 ft., only slightly less than the 1,076 sq. ft. area of the traditional 10 x 10 meter quadrat in forest ecology. These areas are sufficiently close to permit general frequency comparisons with such quadrat data in the literature. If exact equality is desired, quadrat lengths of 53.8 ft. along the strip may be utilized. Curtis and McIntosh (1950) favor adjustment of quadrat sizes to yield frequency data within a predetermined ideal range. The field worker would not know what size to adopt until a number of quadrats had been completed; also larger quadrats might be needed for the less common species than for the dominants, nullifying comparability. The line-strip method offers a practicable means for manipulating quadrat size, since any length of strip-section constituting the quadrat can be selected or varied *a posteriori* as office analyses of the data might dictate.

In applying a line interception method to southwestern desert shrub communities, J. L. Gardner (personal communication 1953) fastens a screen-door spring of the long spiral type to each end of the steel tape, and stakes out the latter with slight tension on the springs. It is thus very convenient to record cover directly, by pulling the tape (on line) to bring an even foot mark to one edge of the crown. The springs incidentally prevent sagging of the tape.

Two general reasons may exist for determining the nature of dispersal. It has intrinsic interest as a characteristic of the population. Secondly, if dispersal can be shown to be random or nearly so, this justifies the application of simple statistical methods based on the assumption of randomness. Such a possibility is desirable at least for establishing sampling adequacy.

The second, perhaps more practical, reason loses importance when the line-strip method is used, since the propriety of using statistical methods may be validated without special attention to dispersal. Navarro, of the Purdue Statistical Laboratory, kindly permits mention of an unpublished conclusion from his work on various mathematical models describing plant dispersal. Of those considered, as the length of the line-strip becomes sufficiently long the probability that the

number of tree centers in the strip takes on any positive integer tends to the Poisson variate. The number of plants per strip would tend to behave in a random manner, *i.e.,* as a Poisson variate. This idea is supported by the density results on white cedar, the only clustered species; its dispersal index of 11 showed a very extreme deviation from randomness. Considering this and its scarcity in the stand, the estimate of 9 trees per acre was very close to the 7 per acre actually present.

The magnitude of the standard errors of various attributes shows that sampling was generally adequate for the dominant species but was questionable for several of the less important species that were considered. The 400 ft. line-strips used were too short. Dice (1952) indicates that, on the assumption of non-randomness, the quadrat size should be sufficient to include ten individuals of a given species per quadrat on the average, but, if randomness is demonstrated, the number included may be smaller. It might be expected from this that a strip should be long enough to average ten trees for each important species. However, because of the effect of very long narrow plots in minimizing the statistical difference between the types of dispersal, considerably fewer than ten trees of a species per strip is adequate even when they are clustered. Eight or more line-strips each at least 600 ft. long, would probably be needed in most stands of complex composition. It is also desirable that the strips collectively include about 15 per cent of the station area. The applicability of these rough rules of thumb will vary with the nature of the stand, the worker's interest in the less common species, and the sampling accuracy required. It would seem that a per cent standard error no higher than 20 might be considered to indicate a generally acceptable sampling adequacy for a species in forest ecology. In sampling as well as this for several subordinate species of a stand, the dominants would usually be sampled considerably better.

Summary

The line-strip sampling unit is a combination of line interception and quadrat methods in which only the line is surveyed. The line-strip method is shown statistically, and by comparison with full tallies, to be suitable for detailed studies in three diverse types of eastern coniferous forests (spruce-fir, red pine-white pine, and jack pine) and in a maple-beech stand. This unit has several important advantages, in both field and office work, over the quadrat as usually applied. It is ideal for permanent marking of sampling units. Strip-quadrats (fractions of the strip) can be varied in length *a posteriori* to make frequency comparisons with publications based on sampling by quadrats of any size not exceeding the strip area. Although the nature of dispersal may be determined, the need for this is much reduced because of a statistical property of very long sample units. The final number of line-strips needed may be calculated after running the first 5 or 6 at a station. Often about 8, each 600 ft. long, covering about 15 per cent of the station area, are required to obtain an acceptable per cent standard error of 20 or less for each significant species. To obtain per cent sampling errors of similar amounts for density, basal area, and cover, the strip width need not exceed 20 ft. for eastern coniferous stands, but should probably be 24 ft. wide for maple-beech. Basal area is much more accurately sampled in coniferous stands than in maple-beech. Although introduced for coniferous stands and mechanically easier to use there, the line-strip method appears to be well-adapted to hardwood stands also, since only in the maple-beech stand were cover errors the lowest ones. The method is rapid, considering the area sampled and the scope of data obtained, and is well-suited for judging sampling adequacy by statistical procedures.

References

Bormann, F. H. 1953. The statistical efficiency of sample plot size and shape in forest ecology. Ecology **34**: 474-487.

Buell, M. F., and J. E. Cantlon. 1950. A study of two communities of the New Jersey pine barrens and a comparison of methods. Ecology **31**: 567-586.

Canfield, R. W. 1941. Application of line interception method in sampling range vegetation. Jour. Forestry **39**: 388-394.

Chisman, H. H., and F. X. Schumacher. 1940. On the tree-area ratio and certain of its applications. Jour. Forestry **38**: 311-317.

Cottam, Grant, J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology **34**: 741-757.

Curtis, J. T., and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology **31**: 434-455.

Dice, L. R. 1952. Natural communities. Univ. Mich. Press, Ann Arbor. 547 p.

Fracker, S. B., and H. A. Brischle. 1944. Measuring the local distribution of *Ribes*. Ecology **25**: 283-303.

Gleason, H. A. 1952. Illustrated flora of the northeastern United States and adjacent Canada. 3 vols. New York Botanical Garden, N. Y.

Grosenbaugh, L. R. 1952. Plotless timber estimates—new, fast, easy. Jour. Forestry **50**: 32-37.

Hoel, P. G. 1943. The accuracy of sampling methods in ecology. Ann. Math. Statistics **14**: 289-300.

Levy, E. B., and E. A. Madden. 1933. The point method of pasture analyses. New Zealand Jour. Agr. **46**: 267-279.

Niering, W. A. 1953. The past and present vegetation of High Point State Park, New Jersey. Ecological Monog. **23**: 127-148.

Penfound, W. T. 1945. A study of phytosociological relationships by means of aggregations of colored cards. Ecology **26**: 38-57.

Toynbee, A. J. 1946. A study of history. Oxford Univ. Press, New York and London.

Weaver, J. E., and F. E. Clements. 1938. Plant ecology. McGraw-Hill Book Co., N. Y. 601 p.

Woodin, H. E., and A. A. Lindsey. 1954. Juniper-pinyon east of the continental divide, as analyzed by the line-strip method. Ecology **35**: 473-489.

NESTING AND PRODUCTION OF THE MOURNING DOVE IN TEXAS[1]

Wendell G. Swank
Arizona Game and Fish Department, Phoenix, Arizona

Introduction

The mourning dove (*Zenaidura macroura*) is one of the principal game species in the Southeast. Its recent apparent decrease in numbers was the impetus that brought about a cooperative study of this species by state wildlife agencies in that region and by the U. S. Fish and Wildlife Service. Apparently the mourning dove population in Texas did not decline to the extent that it did in the Southeast. However, due to insufficient knowledge concerning factors controlling dove populations, no explanations have been offered to account for the drop in population in the Southeast and the apparent lack of a decline in Texas.

The major purpose of this study was to obtain information pertaining to those factors that influence mourning dove populations in Texas. This information is necessary to provide a basis upon which to begin scientific management of this important migratory game bird. This investigation was initiated in the spring of 1949 and was terminated in June 1951.

Data on nesting of the western mourning dove (*Zenaidura macroura marginella*) were taken intensively on an 81-acre study area on the campus of the Agricultural and Mechanical College of Texas. The A. and M. Campus can best be described as a park-like area. Streets were lined with trees that formed a rather high canopy, and the grounds were in lawn. Most of the trees were between 25 and 35 feet tall, and a few, particularly eastern red cedar (*Juniperus virginiana*) and hackberries (*Celtis occidentalis*) reached a height of 45 feet. Of 1,137 trees on the area the composition by species during the time of the study was 63 per cent live oak (*Quercus virginiana*), 18 per cent eastern red cedar, 12 per cent hackberry, 2 per cent chinaberry (*Melia azedarach*), and a small percentage of other species. Approximately one-fourth of the 81-acre area was occupied by buildings and parking areas.

The campus seemed to provide an excellent nesting habitat for mourning doves. The area was clear for a height of eight to twelve feet under the tree canopy, providing an open view on all sides. This seemed to be one of the necessary requirements for ideal nesting habitat. Even doves observed in woodlands traveled to areas with sparse ground cover to gather nesting material. On the study area male doves preferred the gutters of paved streets over adjacent grass-covered sites for collecting nesting material.

The tree canopy, primarily of live oaks, provided excellent supports and protection for nests. The horizontal limbs and numerous diverging small twigs of this species served to anchor the nests in place. Also the live oak contained an abundance of green leaves the year round, which provided protection for early nests constructed before leaves came out on such species as hackberry, chinaberry, and pecan (*Hicoria pecan*).

Water was always available on the campus study area, because lawns were watered when rainfall was insufficient. The excess water collected in small pools and doves were frequently observed coming to them to drink.

Food was available for the birds in areas principally on the west side of the study area. Birds were observed flying in this direction to feed each morning and evening. Much of the food obtained by these birds was natural, but both corn (*Zea mays*) and wheat (*Triticum vulgare*), probably obtained from the feed yard of domestic stock, were found in the crops of nestling doves.

The desirability of the A. and M. College Campus as dove nesting habitat was indicated by the

[1] This is a portion of a dissertation submitted as partial fulfillment for the Doctor of Philosophy degree. Appreciation is expressed to Dr. George A. Petrides and Dr. William B. Davis under whose direction the study was conducted. Students Lytle Blankenship and Tom Hunt aided in gathering data on movement and activities of juvenile birds. The investigation was supported by a grant from the Wildlife Mangement Institute and by the Texas Cooperative Wildlife Research Unit; U. S. Fish and Wildlife Service, Texas Game and Fish Commission, Wildlife Management Institute, and A. and M. College of Texas cooperating.

high population of birds occupying the area. I found no other area that equalled it on a nest-per-acre basis, and students from over all the state of Texas commented upon the high population of doves on the campus as compared with their home localities.

The study area was systematically covered each week during the nesting period. Each nest discovered was plotted on a map, and a numbered thumb tack was stuck in the nest tree at eye level height. These thumb tacks were prepared by removing the coating on the head with sandpaper, writing on the numbers with India ink, allowing the ink to dry, then coating lightly with clear fingernail polish. The number on a tack thus treated was readable throughout the nesting season, and in most cases was still identifiable after one year.

Field notes were transferred to permanent records and filed according to subject. Information on nestings was transferred to McBee Keysort Punch Cards to facilitate final analysis of the data.

Factors Initiating Nesting Activity

Workers in ornithology have attributed the nesting urge of birds in the Northern Hemisphere to such factors as increasing temperatures (Linsdate 1933), light (Rowan 1925, 1927; Bissonnette 1932), and increased activity (Rowan 1928). Type and quantity of food has also been mentioned as a motivating factor (Bissonnette 1932).

Linsdale (1933) pointed out that most workers dealt with a single factor when working on sexual periodicity and that the interrelationship of such factors as genetic make-up, species represented, conditions in the winter homes of the birds, altitude, rainfall, temperature, photoperiodism, and food supply should be considered. His comparison of the nesting season in California and Kansas, both in the same latitude, demonstrates that light alone cannot control the time of the nesting season. Linsdale, substantiating the work of Davis (1933), points out that there seems to be a correlation between availability of food for young birds and time of nesting, and the availability of food, whether of animal or plant material, seems to be obviously and rather directly dependent upon favorable climatic conditions.

Doves do not require insects upon which to feed their young, and at College Station they began nesting at least one month before those species whose young are dependent upon such a diet. By March 15, when English sparrows (*Passer domesticus*) began nesting, many doves already had young. Nests of other species were found on the area as follows: robin (*Turdus migratorius*), March 15; mockingbird (*Mimus polyglottos*), March 25; blue jay (*Cyanocitta cristata*), March 25; cardinal (*Richmondena cardinalis*), April 5; shrike (*Lanius ludovicianus*), April 5; scissor-tailed flycatcher (*Muscivora forficata*), May 13.

Length of Nesting Season

Active dove nests were found in the vicinity of College Station in every month except November and December, but a truly active nesting period can be said to extend only from about March 10 to September 10. The active nesting period is preceded by an extended courtship, the intensity seemingly varying with the weather. In the spring of 1949, I heard the first mourning dove on the campus study area on February 12. On February 14, I heard four doves calling, but on the 15th the weather turned cool and damp. This was followed by a noticeable drop in courtship activity. By February 21 the weather had moderated and dove courtship activity was again evident everywhere. There was an abundance of males on cooing perches giving forth with their loud plaintive calls. On February 23, a pair was observed building a nest, but a period of rainy cold weather began on February 24 and lasted four days, resulting in a noticeable decrease in all nesting activity. This reduced activity lasted until about March 5, when doves were again noticed gathering sticks for nests and carrying on other courtship actions.

Courtship and activities leading up to the 1950 nesting season were similar to those of 1949. One dove was heard calling in the latter part of December for several days in succession, but with the advent of cold rainy weather its courtship activity ceased.

In 1950 a nest was found on February 7 that contained two doves estimated to be two and three days old. Allowing 14 days for incubation would place the date of egg laying on January 25 (Table I).

There is some indication that early nesting birds are those entering their second nesting season, while those that do not nest until the season is well advanced are birds hatched the preceding summer. This statement is based on the following observation on penned birds. An adult male bird captured on the nest in the late summer of 1949 began cooing and carrying on courtship activities around the middle of the following January. A male and a female taken from nests as young birds in the late summer of 1949 did not begin courtship activities until late April 1950. If activity of a similar nature exists in the wild

TABLE I. *Data on nesting of mourning doves on the 81-acre A. and M. campus study area, 1950*

Month	Number of Active Nests	Per Cent of Total	Number Successful	Per Cent Successful	Per Cent Successful of Total Number
January	2	0.31	0	0.0	0.00
February	10	1.54	5	50.0	1.25
March	40	6.17	15	32.5	3.75
April	60	9.26	40	66.7	10.00
May	137	21.14	85	62.0	21.25
June	165	25.46	116	70.3	29.00
July	140	21.60	90	64.3	22.50
August	75	11.57	39	52.0	9.75
September	19	2.93	10	52.6	2.50
Total	648	99.98	400		100.00

the small number of early nests could be attributed to the nesting activity of old birds, and the great increase of nests in late spring and early summer could be attributed to the activity of birds hatched the preceding nesting season.

Termination of the nesting season, like the beginning, is a gradual process. Few nests were begun in Brazos County after September 1 (Table I), but nests begun on that date were active until about October 1. In the last active dove nest found in 1949 the young were fledged on October 23. In 1950, the date of the last young leaving the nest was October 5.

Monthly Nesting Activity

Nesting Activity Based on Wings from Juvenile Birds. In 1949, wings of doves were obtained from Texas hunters. The date of hatching for each of the 728 juvenile birds was estimated by determining the number of the last juvenal primary wing feather that had been replaced by an adult feather, then referring to a graph constructed from molt data for birds of known age (Swank, *in press*). This showed that August contributed the most juvenile birds, that July was a close second, and that June was third (Fig. 1). Very few of the young birds taken were produced in April and October, and September and May combined accounted for 17.4 per cent of the total. If it is assumed that the percentage of juvenile birds in the hunter's bag is indicative of the number of birds produced, a grouping of the same data into ten-day intervals reveals that there was a gradual, unsteady climb in production from April to the latter part of August, then a rather sharp, steady decline to the first of September (Fig. 2).

Nesting information during the 1950 season, based on wings collected from 907 juvenile birds, follows closely that of the 1949 season (Fig. 1). When the data are grouped by months the only

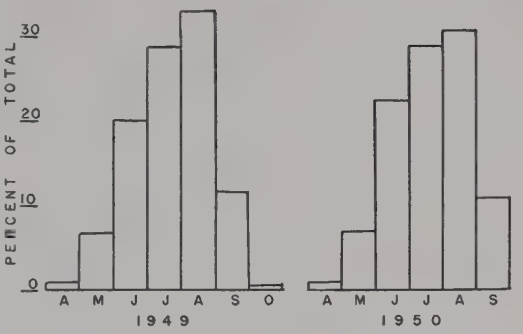


FIG. 1. The production of doves by month based on wings of juvenile doves killed in Texas. Sample size was 728 wings in 1949 and 907 wings in 1950.

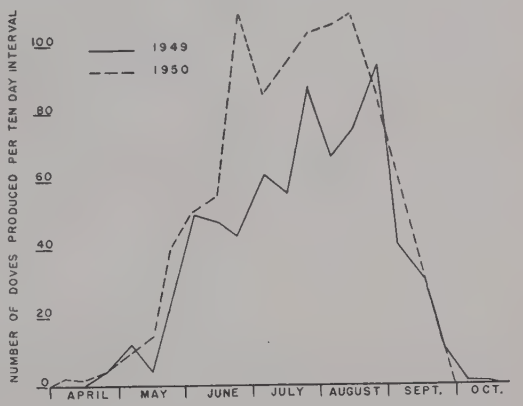


FIG. 2. The production of doves in 1949 and 1950, with nesting season divided into ten-day intervals, based on wings from juvenile doves collected in Texas. Sample size was 728 wings in 1949 and 907 wings in 1950.

difference in the two years is that the number of birds hatched in June in 1950 made up 22.3 per cent, as compared with 19.8 per cent in 1949, and this was balanced by 30.7 per cent in August 1950, as compared with 33.0 per cent in August 1949. These differences are not significant at the 95 per cent confidence level. Data on hatching date of young for 1950 (Fig. 2), grouped into ten-day intervals, follow fairly closely the 1949 data, except for a peak in late June, which is absent in the latter year.

Nesting Activity Based on Nesting Studies. The production of doves in 1950 on the A. and M. campus study area, based on actual hatching date in 442 nests, shows peaks in June and July (Fig. 3). The precentages for May and August are almost equal, and there is little difference between April and September. When the same data are grouped by ten-day intervals (Fig. 4), they show a gradual increase from February to late June and early July, then a rather sharp decline until the latter

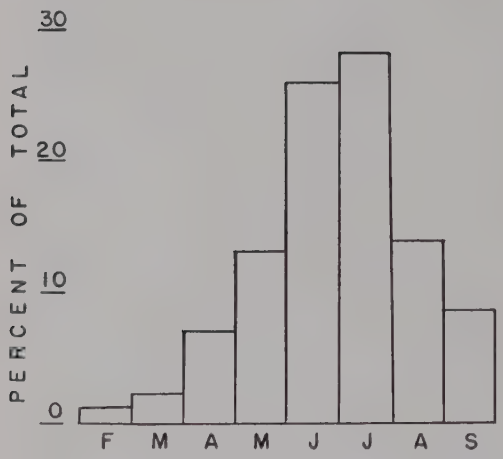


FIG. 3. The production of doves on the A. and M. Campus Study Area, 1950, based on date of hatching in 442 nests.

part of September when the last young left the nest.

FIG. 4. The production of doves in 1950 on the A. and M. Campus Study Area, divided into ten-day intervals, based on date of hatching in 442 nests.

On June 20, near the height of the nesting season, there were 123 active nests on the 81-acre study area.

Nesting Activity Data from Wings Versus Nesting Studies. A comparison of the data from wings sent in by hunters with those data obtained on the A. and M. campus study area reveals that the general nesting season and peaks of production as calculated from bag records are about a month later than those obtained on the study area (Fig. 5). It is unknown why this discrepancy should exist, but there are four possible factors that should be considered. First, the doves whose ages were determined from wings were taken from various locations throughout Texas, and it is possible that a higher proportion of doves, on the whole, are produced later in other sections than at College Station. Note (Fig. 6) that in Throckmorton County, Texas, Jackson (1941) found almost as many nests in August as in July, the peak month; and Monk (1949) in Tennessee found that 20 per cent of the total nests occurred in August. It is also significant to note that almost all workers have found that of those nests present a higher percentage are successful in the latter part of the season.

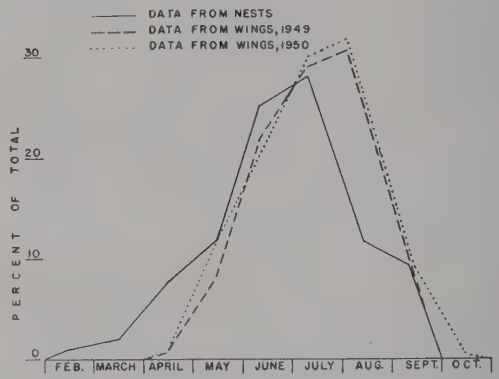


FIG. 5. Date of hatching of doves based on data from nests at College Station and from wings collected by Texas hunters.

Second, those wings analyzed were from juvenile doves taken by hunters. Both band returns and observations indicate that the younger animals are less wary than are older ones. It is therefore possible that a higher proportion of the younger birds was taken than actually existed in the population.

A third factor to be considered is that the technique used to ascertain the age may fix the age of a bird younger than it actually is. This fact cannot be discounted, and more data are needed before the technique employed can be used with complete confidence.

The fourth point that may lead to the difference between the height of nesting seasons obtained by the two methods is that at the beginning of the hunting season natural mortality factors have been acting on those birds hatched early in the nesting season longer than on those hatched late in the season. Austin's (1951) rather extensive data show that the annual mortality of juvenile doves banded on Cape Cod amounted to 73.8 per cent. Limited data from this study indicate that by the end of one year 86 per cent of the doves banded as juveniles at College Station have passed out of the population. Using Austin's more conservative figure, and assuming that mortality the first six months of life is at least as great as the second six months, of 100 flying juvenile

birds born in April, only 70 would be available to hunters. Of 100 flying juveniles born in August, 94 would still be living by September 1, thus available when hunting season began.

Nesting Activity at College Station as Compared with Other Areas. The monthly nesting activity of doves on the A. and M. Campus agrees rather well with nesting activity obtained by Jackson (1941) in Throckmorton County, Texas (Fig. 6).

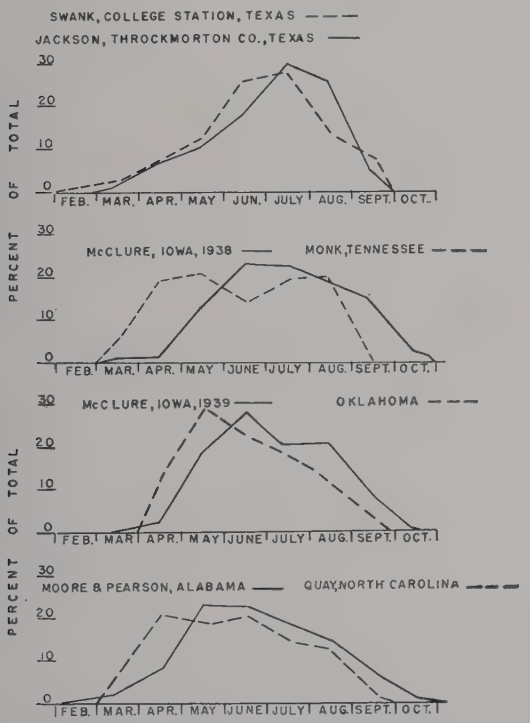


FIG. 6. Nesting intensity of mourning doves by month at different locations in the United States.

Nesting activity began earlier at College Station, which can perhaps be explained by the abundance of evergreen live oaks for nesting sites, whereas Jackson was working in an area where most of the doves nested in deciduous mesquite (*Prosopis chilensis*). That doves prefer to nest in trees with foliage has been previously pointed out by Pearson and Moore (1939). This is substantiated by my data which show that at College Station of 112 nests located up to May 1 only five (4.5 per cent) were in deciduous species, but over the whole season aproximately 20 per cent of the nests occurred in trees that normally are bare of leaves during the winter months. For April, the percentage of nestings occurring at College Station coincided with information obtained by Jackson, but there was a slight gain in activity on the A. and M. Campus Area during May, and a considerable gain in June over Jackson's data. From June the nestings in Throckmorton County climbed to a rather sharp peak in July, tapered off slightly in August, then dropped rapidly to September. The College Station data show a rapid climb from May to June, a slight increase in July, then a sudden drop in August and a tapering off in September.

A comparison of nesting activity in Texas with that in other states shows that the peak of nesting is approximately a month later than that obtained elsewhere (Fig. 6). McClure's (1943) data for both the 1938 and 1939 nesting seasons in Iowa show peaks in June. Data by Monk (1949) in Tennessee and Quay (1951) in North Carolina both show a high percentage of the total nestings as early as April, three months before the nesting peak occurs in Texas. Data from Oklahoma by Nice (1922-23) show that the peak occurs in May with a rather sharp decline on each side. It is interesting to note that McClure's data for doves in Iowa for 1938 and 1939, and Moore and Pearson's data for Alabama more closely follow those of Texas than those obtained by Nice, yet geographically, Oklahoma is closer than either Iowa or Alabama.

In the above comparison of dove nesting activity at College Station with other areas, limitations should be noted. Data herein presented are, for the most part, from a single nesting season and the fallacy of using one season as a representation of what usually occurs can be demonstrated by comparing the data of McClure for the seasons 1938 and 1939. In 1938 the percentage of the total of active nests during June and July remained practically stable at 23 per cent, but in 1939, May had 18 per cent of the nests, July 20 per cent, and June produced a distinct nesting peak between the two at 28 per cent. McClure attributes the lack of a June peak in 1938 to the loss of nests during unusually stormy weather in that month of that year.

It appears then, that to compare monthly nesting activity at one location with another it is desirable to gather data over several years and to establish a mean. It is also necessary to consider those various factors affecting nesting activity such as light, altitude, weather, suitability of nesting grounds, and perhaps the ratio of the various age classes making up the breeding population.

Biology of a Nesting Population

Establishment of Territory. Doves announce their arrival on the nesting ground by early-morning and late-evening cooing of the male. Often a tree

or an electric wire is selected as a perch and frequently between calls he leaves his perch with a few fast strokes of the wings. After obtaining momentum and some altitude, he sails on outstretched set wings in a wide circle and again comes back to his perch.

Defense of territory is displayed by doves only at certain locations. For instance, if, during the territory establishment stage, another male dove encroaches upon defended territory, the resident bird crowds out the intruder by flying over and attempting to alight on him. If this does not indicate to the intruding bird that he is unwanted, the resident bird moves close and gives him a sharp blow with the wing. This usually convinces him that it is best to move on.

Resident male doves tolerate no intrusion by other doves into areas near their cooing perch or into the area where they are searching for nest materials. Many times I have observed a male dove interrupt his search for nesting material and fly 20 to 30 feet to harass an intruding male until it was driven away.

Once the nest is established and incubation is begun, defense of territory near the nest is practically eliminated. Foreign doves have been observed to alight within a few feet of a nest without being attacked by the resident birds. Another observation that emphasizes the lack of territorial defense by doves is that two active dove nests were frequently found in the same tree, and once three nests, all active, were in one tree. In no instance, however, were nests in the same stage of development found close together. This indicates that territorial tendencies prevent two pairs from building nests close together during the same period, but that once a nest is established the defense of the territory near the nest is abandoned.

As the season progressed at College Station, male doves spent less time cooing and establishing territories between broods. In the early mornings of April and May calling doves were everywhere on the area but by the middle of August only occasionally was a dove heard. This reduced activity did not indicate, however, that nesting had stopped, because as many active nests were found in August as in May (Fig. 3).

Number of Active Dove Nests on the Area. Only during 1950 was it possible to take complete data on the number of active nests on the 81-acre study area. A total of 648 nests were found (Table I). Although complete data were not taken during the 1949 nesting season, the information collected indicates that the nesting population was about the same as for the 1950 nesting season. This statement is based on counts of active nests on a two-block area during both years. On this two-block area in 1949 on May 15 there were 24 active nests and in 1950 on the same date there were 25 active nests.

Indications are that the nesting population in 1951 was much smaller than in 1950. In the first week in June 1950, there were 89 active nests on the campus study area; during the same period in 1951 there were only 26 active nests. This decrease in nesting population was believed to be due partially to a severe ice storm in early February that prevented birds from getting food for several days. Freezing conditions extended into the major wintering ground of the doves from Kentucky through Tennessee, Mississippi, Louisiana, and Texas into the Rio Grande Valley and northern Mexico. At College Station the frozen bodies of four doves, two mocking-birds, two starlings, and two myrtle warblers were found.

Data Obtained from Marked Birds. During the nesting season of 1950, by use of a nest trap (Swank 1952) 93 adult doves were captured on active nests and marked. It was physically impossible to follow the activities of many of these birds, so major emphasis was placed on keeping accurate data on 11 that were trapped early in the nesting season (Fig. 7). These birds included four pairs with both male and female marked, two females with their mates not marked and one male with its mate not marked. Observations on other marked individuals served to substantiate many of the conclusions drawn from the activities of these 11 birds.

(1) *Number of nesting attempts per pair.* Birds of pair A (Table II) were trapped on the nest and marked on May 6. During this nesting season six known nesting attempts, including the one on which the birds were trapped, were made by this pair. Pair B (Fig. 7) also made six known attempts at nesting. Pair C made five attempts at nesting, and pairs D and E each made four. Pairs F and G each made and successfully completed only three known attempts.

In addition to the six known nestings I believe Pair A made an attempt at nesting before they were marked. The basis for this assumption is that after this pair was marked they nested three times in a nest in which a clutch of eggs was destroyed prior to the capture of this pair. As will be shown later, several nestings in the same nest may not all be made by a single pair, but there is a tendency for a pair to return to a nest previously used.

A nest was not found for Pair C from June 1 to July 3, which is about the length of time required for a nesting. Pair D escaped observation

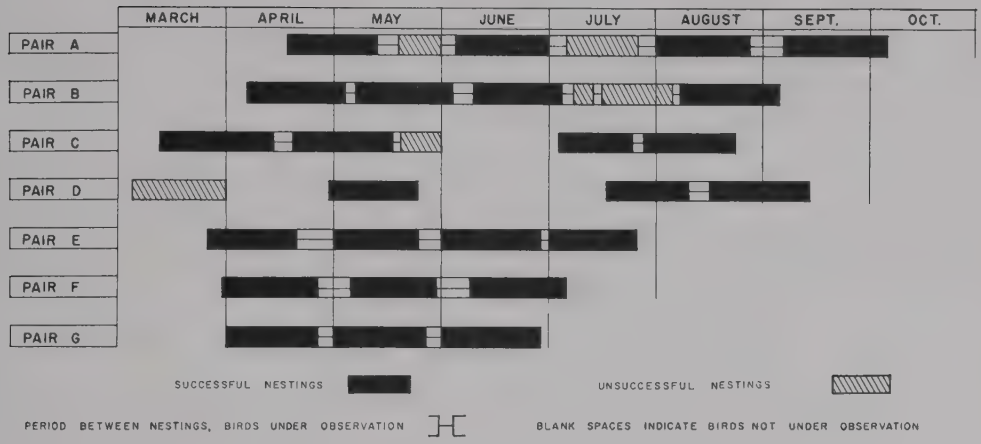


FIG. 7. Nesting activities of seven pairs of marked mourning doves, College Station, Texas, 1950.

for two periods: from April 1 to April 29, and from May 27 to July 17. Additional nesting attempts could have been made during both of these periods.

It seems entirely possible that these marked pairs could have nested off the study area during the periods that they were not under observation; or they could have nested on the area and in spite of a diligent search their nests could have remained undiscovered. This possibility cannot be dismissed, for upon several occasions nests were not discovered until the young were about to leave.

To summarize, we can state definitely that of the birds marked, representing seven pairs, two made six nesting attempts, one made five, two made four, and two made three, for a total of 31 nesting attempts. Using these data, the average number of nesting attempts per pair for the 1950 season was 4.4. Circumstances indicate that two of these pairs made one more nesting attempt and another possibly made two additional attempts. This makes a total of 35 attempts or 5.0 attempts per pair. The number of nestings attempted by doves at College Station closely approaches that found by other workers. McClure (1943) concluded that in Iowa the mourning doves attempted an average of 5.4 nestings in 1938, and 5.1 nestings in 1939. Webb (1949) in Ohio found that doves have about four broods per year, and Nice (1923) in Oklahoma calculated that to maintain a stable population, doves must attempt at least three nestings. It is of interest to note that the data of Whitman (1919), from the nestings of nine pairs of penned mourning doves, show that the number of nesting attempts varied from two to seven and averaged 4.4, the same number as that obtained at College Station.

(2) *Successful nestings.* Four pairs had four known successful nestings, a nesting being considered successful if at least one young reached fledgling stage. The other three pairs each had three successful nestings. The success of all known nesting attempts of these marked pairs averaged 80 per cent. These marked pairs were unusually successful, for the average success of 648 known attempts on the study area during the 1950 nesting season was only 61.7 per cent.

(3) *The nesting cycle.* The mourning dove has an approximate 30-day nesting cycle, composed of 14 days for incubation, 11-15 days for young to reach fledgling stage, and from two to eight days after young leave the nest before eggs for a new clutch are laid. The period from one clutch of eggs to another, for 14 nests that were successful, varied from 25 to 38 days, averaging 31.8, and with a standard deviation of $\pm$ 3.02.

When eggs or young are destroyed very little time elapses before the nesting cycle is again imitiated. In one instance, on June 1, eggs had been incubated 12 days when the nest was destroyed by removal of the nest tree by a construction crew. Three days later a new nest built by this pair contained one egg, and the other was laid the following day. On July 13, another pair had its eggs destroyed after incubating them for six days. Their new nest was not found immediately, but on the basis of a 14-day incubation period the eggs were laid two and three days, respectively, after destruction of their former clutch.

In another instance a nest contained a seven-day-old bird when it was abandoned because of unusually persistent trapping attempts. Five days later this pair had two eggs in a nest that they had used previously.

From these data which present three different stages of nesting cycle interruption, it appears that when nests are destroyed, mourning doves can lay a new clutch of eggs within two to five days, regardless of the stage of nesting cycle when the interruption occurs. Guthbert (1945), in his work on the ovarian cycle of the ring dove (*Streptopelia risoria*), a species whose nesting cycle is similar to that of the mourning dove, found that laying usually occurred again about six days after breaking up of a nest, regardless of the point at which the eggs or young were removed.

(4) *Distance moved between nestings.* The nesting area used by a pair of doves throughout one reproductive season seemed to be rather small. The greatest distance discovered between nests built by one pair of doves was about 800 feet. In most cases, however, the distance between subsequent nests did not exceed 200 feet. One pair of birds (Pair F, Table II) raised three consecutive broods in one nest. Another pair alternated between two nests in the same tree for four nestings, moved 400 feet for the fifth nesting, then moved back to one of the original nests for the sixth attempt.

Of the 31 known nesting attempts for the seven

TABLE II. *Chronological nesting activities of seven marked pairs of mourning doves*

Nest No.	Location of Nest in Relation to Last Nest	Approximate Date Eggs Laid	Number of Eggs Laid	Nesting Success	Adults Last Seen with Young	Remarks
			Pair A			
1	Birds trapped on this nest on May 6. Nest in cedar tree. Contained one young six days old.	April 16	2	One young left nest May 13.	May 13	Young 13 days old when last observed on nest.
2	25 ft. north of nest 1 in same row of trees. Nest in cedar tree.	May 19	2	Destroyed June 1. Tree removed.		Male observed 7:30 a.m. May 18, gathering nesting material. May 19, 2 eggs.
3	250 ft. southwest of Nest 2. Live oak tree.	June 4	2	Two young left nest July 1.	July 2	Young 12 days old when last observed on nest.
4	300 ft. northeast and 50 ft. east of nests 1 and 2. Nest in hackberry tree. This nest formerly occupied by another pair of mourning doves.	July 5	2	Nest destroyed July 26.		Nest contained one young 7 days old when destroyed
5	Same as No. 3.	August 1	2	Two young left nest August 28.	August 28	Young 12 days old when last observed on nest.
6	Same as Nos. 3 and 5.	Sept. 6	2	Two young left nest October 5.	October 5	Young 12 days old when last observed on nest.
			Pair B			
1	Birds trapped on this nest on April 29. Nest contained one young 9 days old.	April 6	1	One young left nest May 3.	May 9	Young 13 days old when last observed on nest. Young and adult in tree near nest May 9, 7:45 a.m.
2	Same tree, different nest. Nesting attempted in this same nest, but destroyed on March 31. Probably this pair of birds.	May 6	2	Two young left nest June 3.	June 9	Young 14 days old when last observed.
3	Same as No. 1.	June 9	2	Two young left nest July 4.	July 4	Young 11 days old when last observed on nest.
4	Same as No. 2.	July 7	2	Destroyed July 13.		Eggs incubated 6 days when nest destroyed.
5	400 ft. south of nest 4 in cedar tree.	July 15	1	Abandoned due to activities of investigator, August 5.		Young raised to 7 days then nest abandoned. Trapped and remarked male. Female would not enter trap.
6	Same as Nos. 2 and 4.	August 7	2	Two young left nest September 5.	Sept. 5	Young 15 days old when last observed on nest.

TABLE II.—*Continued*

Nest No.	Location of Nest in Relation to Last Nest	Approximate Date Eggs Laid	Number of Eggs Laid	Nesting Success	Adults Last Seen with Young	Remarks
			Pair C			
1	Bird trapped on this nest.	March 12	2	Two young left nest.	April 14	
2	50 ft. east of nest 1, same side of same street.	April 20	2	Two young left nest.	May 18	
3	Same as nest 2.	May 20	2	Destroyed June 1.		
4	225 ft. northwest of nest 3.	July 3	2	One young left nest.	July 25	
5	200 ft. north of nest 4 and 450 ft. northwest of nest 1.	July 28	2	Two young left nest.	August 24	
			Pair D			
1	Birds trapped on this nest.	March 4	2	Destroyed April 1.		Nest destroyed by wind. Two young died on ground.
2	100 ft. west of nest 1, same street, opposite side.	April 29	2	Two young left nest May 25	May 27	
3	800 ft. north of nest 2.	July 17	2	Two young left nest August 10.	August 10	
4	100 ft. southwest of nest 3.	August 16	2	Two young left nest.	Sept. 14	
			Pair E			
1	Bird trapped on this nest.	March 26	1	One young left nest April 21.	April 24	
2	30 ft. west of nest 1, same side of same street.	April 30	2	Two young left nest May 25.	May 25	
3	200 ft. west of nest 2, other side of same street.	June 1	2	Two young left nest June 28.	June 30	Saw adults gathering nesting material for new nest while still feeding young in this nest.
4	Same nest as No. 2.	July 1	2	Two young left nest.	July 26	
			Pair F			
1	Birds trapped on this nest.	March 30	2	Two young left nest April 27.	April 28	
2	Same nest as No. 1.	May 5	2	Two young left nest May 30.	May 31	
3	Same nest as Nos. 1 and 2.	June 8	2	Two young left nest July 3.	July 5	
			Pair G			
1	Bird trapped on this nest.	April 1	2	Two young left nest April 27.	April 27	
2	50 ft. north of nest 1, same side of street.	April 30	2	Two young left nest May 26.	May 26	
	100 ft. southeast of nest 2, 75 ft. east of nest 1.	May 30	2	Two young left nest June 26.	June 28	

pairs, seven were in the nest on which the birds were trapped, 14 attempts were made in nests new to the birds, five attempts were made in nests used previously by that pair but not during the preceding nesting, four were in the same nest as the last nesting, and one was made in a new nest, but in the same tree as the last nesting (Table II).

Although there is a tendency for a pair of doves to use a nest they have previously occupied, it is not reliable to use the number of broods raised in one nest as the number of broods reared by one pair. Several times unmarked birds used nests formerly occupied by marked ones, and once a marked pair used a nest previously used by unmarked birds.

(5) *Daily movement.* Marked birds were frequently observed in a cultivated area about one mile west of the study area, and twice marked individuals were seen in the vicinity of Easterwood airport, approximately three miles west of the campus.

(6) *Permanency of pairing.* Evidence from marked pairs indicates that doves stay paired at least for the one season. Of those where both birds of a pair were marked no changing of mates was noted.

Number of Young Produced to Fledgling Age.

(1) *Production by marked birds.* Of the seven marked pairs followed throughout the nesting season of 1950, five produced seven young to fledgling stage, and the other two produced six each. This is an average of 6.7 young per adult female. I believe this is greater than the average production. This relatively high figure can perhaps be explained by the chance selection of birds that nested over a longer period than the average. That is, these marked birds were selected early in the nesting season and perhaps they had more nestings than the average pair. It is also pertinent to point out that these birds suffered only a 20 per cent mortality of nestings, while the average for the study area in 1950 was 38.3 per cent. Again, the only possible explanation, other than chance alone, is that the birds selected early were in their second nesting season, thus they were more experienced and possibly more successful nesters.

(2) *Number of young produced as determined by wing analysis.* The number of young produced per adult, as determined from analysis of wings from 728 doves taken in Texas during the hunting season of 1949 was 1.67. Pearson and Moore (1941) in Alabama found the sex ratio of doves to be almost evenly divided. If we assume that this condition existed in Texas, each female during the nesting season of 1949 was successful in producing to a huntable age 3.34 young. In 1950, under the same assumption, analysis of 907 wings showed that each female was successful in producing 3.04 young.

The actual production of young per adult female was probably somewhat higher than this, because data on most species show that mortality factors operating from the time of flying until the hunting season take a higher proportion of juveniles than adults. Our band returns showed no significant difference in survival of nestlings banded just before leaving the nest, birds banded as flying juveniles, and those banded as nesting adults. Our data, however, were limited, since we received returns on only five birds banded as adults, 11 banded as flying juveniles, and 56 banded as nestlings.

Analysis of returns of doves banded at College Station shows that mortality the first year was 86 per cent, and declined to about 45 per cent the second and third year. Heavy mortality indicated for first year birds is believed to be due to the great number of doves banded in 1950 that died during severe weather in February of 1951. Austin (1951) in his analysis of 2,690 mourning doves banded on Cape Cod, Massachusetts, over a period of 21 years came to the conclusion that annual mortality was about 80 per cent the first year of life after leaving the nest, and declined to about 55 per cent yearly thereafter.

Management Significance

Dove nesting, hence dove production, is influenced by many factors. Data taken during this study on some of these factors permit us to draw the following conclusions relative to dove management.

(1) Park-like areas are usually excellent dove nesting habitat. Such areas are even more desirable if a large proportion of the trees are of the broad-leaf evergreen type. Trees of this type provide protection for early nests constructed before leaves develop on most deciduous species.

(2) An extended cold, wet spring may inhibit early nesting activities. Hence reduce the number of young birds produced.

(3) At College Station, Texas doves hatched in May, June, and July made up 72.75 per cent of the total, hence any catastrophe such as severe storms or forest fires occurring during these months would considerably curtain the annual production in the areas affected.

(4) Some doves are still nesting when the hunting season begins in September, but doves hatched during this month made up only two and one-half per cent of the total annual production.

(5) By their territorial defense around cooing perches and around nest material hunting grounds, male doves limit the number of pairs nesting in an area.

(6) Dove nesting populations may fluctuate greatly. An unusually cold period may take a heavy toll of wintering birds, hence reduce the number of nesting birds the following summer. The taking of annual population surveys just prior to the establishment of hunting regulations is a necessity. Such surveys would provide information upon which to base regulations governing the extent of dove harvest.

(7) Seven pairs of marked birds reared to the fledgling stage an average of 6.7 young. If we assume that production equals mortality, annual turnover of the dove population amounts to 77 per cent.

(8) Of those birds taken by hunters during the season, at which time most juvenile doves are well awing, birds of the year constituted approximately 60 per cent. Hence, if we assume that the number of new birds entering the population equals the number passing out of the population, for every ten birds present in September only four will be alive at the end of the following nesting season.

Summary

Mourning dove nesting studies were conducted during a portion of 1949 and 1951 and all of 1950 in the vicinity of College Station, Texas. The campus of the Agricultural and Mechanical College of Texas was excellent dove nesting habitat. For nest sites doves showed a preference for trees which contained leaves over trees which had not yet leafed out.

Active nests were found in every month except November and December, but a truly active nesting period can be said to extend only from about March 10 to September 10. Of the nestings in which young were successfully reared to the fledgling stage those during May, June, and July made up 72 per cent of the total.

The number of nesting pairs on the area was in part limited by the territorial defense of the male of cooing perches and of nest material hunting grounds.

The first week in June in 1950 there were 89 active mourning dove nests on an 81 acre study area. During the complete 1950 nesting season a total of 648 active nests were found on the area. In the first week in June in 1951 only 26 active nests were found. The decrease was attributed at least in part to a heavy winter-kill of doves the preceding February.

From the number of young reared to fledgling stage by marked birds, the annual production was calculated to have been 77 per cent. Analysis of wings in hunter's bags showed that in September and October approximately 60 per cent of the population were birds of the year.

Limited band returns indicate that first year birds from College Station had an 86 per cent mortality rate and older birds had a mortality rate of 45 per cent. The heavy mortality indicated for the first year birds is believed to be due to the great number of birds banded in 1950 that died during severe weather in 1951.

Seven pairs of marked birds each reared to the flying stage an average of 6.7 young. Wings of doves taken by hunters in September and October showed an average of 3.34 young per pair of adults in 1949 and 3.04 young per pair of adults in 1950.

Data obtained from seven pairs of marked birds show that the distance between different nesting locations for a pair of doves rarely exceeds 200 feet.

References

Austin, O. L. 1951. The mourning dove on Cape Cod. Bird-banding, **22**: 149-174.

Bissonnette, T. H. 1930. Studies on the sexual cycle in birds. Amer. Jour. Anat., **45**: 289-305.

———. 1932. Light or exercise as factors in sexual periodicity in birds? Science, **76**: 253-255.

———. 1932. Light and diet as factors in relation to sexual periodicity. Nature, **129**: 12.

Cuthbert, N. L. 1945. The ovarian cycle of the ring dove (*Streptopelia risoria*). Jour. Morph., **77**: 351-377.

Davis, W. B. 1933. The span of the nesting season of birds in Butte County, California, in relation to their food. Condor, **35**: 151-154.

Jackson, A. S. 1941. The mourning dove in Throckmorton County, Texas. Thesis for the degree of Master of Science, A. and M. College of Texas, College Station, Texas.

Linsdale, J. M. 1933. The nesting season of birds in Doniphan County, Kansas. Condor, **35**: 155-160.

McClure, H. E. 1943. Ecology and management of the mourning dove (*Zenaidura macroura*) in Cass County, Iowa. Agri. Exp. Stat., Iowa State College, Research Bull. 310: 359-416.

Monk, H. C. 1949. Nesting of the mourning dove at Nashville. Migrant, **20**: 1-9.

Nice, M. M. 1922-1923. A study of the nesting of mourning doves. Auk, **39**: 457-474; **40**: 37-58.

Pearson, A. M. and G. C. Moore. 1939. Nesting habits of the mourning dove in Alabama. Trans. Fourth N. A. Wildl. Conf., pp. 468-473.

———. 1941. Dove sex ratio found almost evenly divided. Alabama Conservationist, May, p. 8.

Quay, T. L. 1951. Mourning dove studies in North Carolina. North Carolina Wildlife Resources Commission, Raleigh, N. C., 90 pp., illus.

Rowan, William. 1925. Relation of light to bird migration and developmental changes. Nature, **115**: 494-495.

———. 1927. Migration and reproductive rhythm in birds. Nature, **119**: 351-352.

———. 1928. Reproductive rhythm in birds. Nature, **122**: 11-12.

Swank, W. G. 1952. Trapping and marking of adult nesting doves. Jour. Wildl. Mgt., **16**: 87-90.

Webb, Lloyd G. 1949. Life history and status of the mourning dove in Ohio. Doctorate dissertation, Ohio State University, Cleveland, Ohio.

Whitman, C. O. 1919. Inheritance, fertility, and dominance of sex and color in hybrids of wild species of pigeons. Vol. 2. Carnegie Inst. of Wash., Washington, D. C., 223 pp.

NOTES AND COMMENT

THE pH/pC CONCEPT

In his note on "Reaction of Soils" (Wilde 1954), Wilde of Wisconsin mentioned several matters which have exercised us for some years and have been the basis of work in this College. The fact that Sørensen used values of electrical conductivity of solutions, and that he employed simple proportion to calculate therefrom the hydrogen-ion concentrations basal to his classical work published in 1909, is enough to indicate the fundamental utility of the quantitative relations between ions and electrical conductivity. The fundamentality of such relations seems to have been generally lost from sight—possibly having been obscured by incorrect teaching.

Wilde has performed a service by publishing the idea that pH of complex and heterogeneous solutions such as those of soil and plant sap is essentially a potentiometric reading: *i.e.*, a reading of electromotive force in volts (E). Since (electrical) conductivity is the reciprocal of resistance, R, the electrical state of an aqueous solution or phase is of the form ER; and it would be well to drop the notion that, except for the simplest solutions of known composition, measured "pH" is anything but a stand-in for an unknowable hydrogen-ion concentration.

By employing inverse logarithmic notations corresponding to the pH notation, a high degree of fresh insight into the behavior of aqueous solutions and suspensions can be obtained through combining pN (normality) with pC (measured electrical conductivity) and pH (measured in any convenient fashion) (Whittles and Schofield-Palmer 1951). Additional plant-physiological and microbiological information can be won by linking these with the pF scale (Schofield 1935) of free energy of aqueous systems. It was suggested (Mattson 1940) that, in soil, pH and pF are linked; but the link could not be made useful before the role of conductivity was apprehended so that pC was brought in.

The pC notation was introduced in 1935 by my former colleague and soil chemist, Dr. C. L. Whittles. It was originally nothing more than a convenient notation for expressing the results of such conductivity-measurements of salinity as have long been made on soils and other materials. About 1949, Mr. Schofield-Palmer perceived that the notation permitted the combination of results of physico-chemical manifestations which had come to be treated of singly (like pH) or separately (when pH, and/or conductivity or osmotic pressure were recorded). Such manifestations are all interlinked and interdependent. First results of this combinatorial idea were given by Whittles and Schofield-Palmer (1951).

The outcome of thus going back to first principles promises to be very fruitful, not only for work with soils proper but also for elucidating equilibrium phenomena necessarily encountered in base-exchange work and in analysis of soils for "available" or extractable phosphate, where the results are not entities but are the resultants of the interplay of a large number of variable factors. Both practically and conceptually, it is impossible to isolate these factors or their effects. The pH/pC concept does not attempt the impossible, but aims directly at measuring and combining what can be readily measured or known.

If the argument is restricted, for the present, to such equilibria of solvent, solute, and colloid as are met with in considering an analytical operation on soil to determine an ion-exchange capacity or the quantity of an extractable ion, it will be clear that the point of equilibrium—and hence the reported result—will be set by the pH, pC, and pN of the extractant (water or other) as well as by the pH and pC of the soil *and also* by the interactions of these with each other. Thus, values obtained from determinations of "exchangeable base" or the like are not entities, but are set and defined by the physico-chemical conditions of the analysis. Consequently, a mere specification of pH and composition of an extractant is not very helpful.

Though the interactions are complex, their resultant in a solution free from non-electrolytes is easily measured in the electrical terms of pH and pC. The pH/pC concept could be equally well, and perhaps more fittingly, expressed in terms of volts and ohms. The term "pH" is here used without engagement about hydrogen-ion concentration; it is simply to avoid making a break with tradition that the "pH" notation has been retained.

The cardinal point of the pH/pC concept is that the concentration and effect of every ion depends on the interactions of water, solutes, and colloids (if any) in a solution. As far as water and simple inorganic solutes are concerned, this was well known to Sørensen—who made it the basis of his determination of the ionic product of water. Thus, pH depends on conductivity; and so far are considerations of conductivity from being a novelty in relation to pH, that their "introduction" now is nothing more than a re-introduction: it relies for its justification on the bases of the ionic theory. In a closed equilibrating system, pH and pC are interdependent. The pF or free energy also depends on pC (Whittles and Schofield-Palmer 1951); thus pF "depends" on pH.

For the system soil/water, it is well-known that the pH, as measured, depends on the ratio of soil to water at which the measurement is made. It is less well-known that if air-dry soil is suspended in ordinary distilled water (as normally used in equilibrium with atmospheric carbon dioxide) then, between the ratios of soil: water approximately from 2 to 10, the pC alters correspondingly with the pH. This was elicited by Schofield-Palmer (Nicol 1954). At lower ratios, the equilibrium may be incomplete; at higher ratios, dissolved carbon dioxide begins to interfere. Within the stated limits of soil to water, the value of the expression 2pH—pC is a constant which is characteristic of the sample. This constant has been denoted pL (Nicol and Schofield-Palmer 1952).

The coefficient 2 is a valency-factor and may be taken as representing carbonate or other divalent ion. For an air-dry sample of soil saturated under field conditions with calcium carbonate and having only the proportions of monovalent ions (H, OH, Na, K) normal to soils of humid climates, it can be shown that pL measured at about 1 : 2½ or 1 : 5 soil : water ratio, cannot exceed about 12.45. This value has been experimentally confirmed.

It follows that for acid soils, the difference between 12.45 and their pL is a logarithmic measure of lime-requirement (Nicol and Schofield-Palmer 1952); whilst for alkaline soils, the excess of their pL beyond 12.45 is a measure of disturbance of the desirable state of predominance of divalent cations, that results from the occurrence of monovalent ions in excess of the amounts

tolerated by "ordinary" plants. These monovalent ions will commonly be ,OH (formally alkaline soils), Na ("saline" soils) or both (alkaline-saline soils). Thus, the pH/pC concept not only provides in pL a numerical characteristic of soil horizons (Nicol 1954) but also gives a new and simple approach to questions of relationships of plants to the physico-chemical state of any soil.

The conditions in arid "saline" soils are often so different from those which obtain in many near-neutral halophytic environments that new terminology seems necessary to avoid confusion: especially since the impedance to growth of non-halophytic plants that is presented by many so-called "saline" soils and waters may be predominantly alkalinity. The terms *hypoplectic* and *hyperplectic,* which are partly mnemonic and refer to interweaving, are suggested to denote soils of which the pL, when ascertained as described above, is respectively less and greater than 12.45. The word *isoplectic* will also be useful.

The pH/pC concept cannot offer direct information about the nutrient or toxic status of a soil, except in so far as (say) a deficiency of potassium or an excess of borate will affect pH and pC. Nevertheless, the potentialities of the combination of pH with pC and with other expressions of physico-chemical manifestations will be evident. The application to nutrient-culture solutions should be obvious.

Much of what in the literature has passed for pH-effects is really the joint effects of pC and pH, or of pH and total osmotic pressure. In any medium—soil or other—such turgor-responses as wilting are responses to pF or osmotic pressure: which is to say, to the inextricable effects of the actions of colloids and electrolytes, aided, in some solutions such as sap and milk, by dissolved non-electrolytes. When soluble non-electrolytes are absent, the essentially physico-chemical effects are naturally integrated into some function of pH and pC. pL of soil is a type of these integrating functions—provided it is ascertained in the manner prescribed. It falls to workers with different classes of natural and industrial solutions to evaluate for themselves the pH/pC function which is most useful. Unless such functions are rationally based there is a risk that they may be of merely local or empirical utility.

The pH/pL "Spectrum"

Some bacteria tolerate and indeed seem to require, an environment of very low pC corresponding to a saturated solution of sodium chloride; but the majority of organisms live within the relatively narrow range of environmental osmotic pressures of the order of from 0.1-0.5 atmospheres or around pC 4 (river organisms; most crop and forest plants) to those of undiluted sea water: up to 26 atm.; pC 1.3-1.4.

The wilting-point of most crop plants and others accustomed to a pC not often below about 3.5 is of the order 15-20 atm. A working value for pF at the wilting-point is 4.2 (da Costa 1938). This is about pC 1.55; since pC = 5.74 — pF = 2.74 — log [osmotic pressure in atm.] (Whittles and Schofield-Palmer 1951). Terrestrial halophytic plants can tolerate a measured soil salinity within the range pC 1.55-1.4 approximately. It will be noted that if ocean water is diluted 2½ times to put its pC-determination on the basis adopted for air-dry soil, its osmotic pressure is reduced to 10 atm., just bringing it within the physical tolerance of land plants. The pC of sea-water diluted 2½ times would be about 1.8; *i.e.*, $\log_{10}$ 2.5, or about 0.4 units, greater than the pC of the undiluted water; the dilution would also operate a pH-change.

From such considerations, it becomes possible to draw, for aqueous systems free from appreciable amounts of non-electrolytes, a straight-line band or spectrum which shows in terms of pH and pC or pF—that is, in terms of pL—the entire range over which plant growth is possible. The sides of the band may also be drawn at any desired or less extreme limits so as to include, for example, such ranges as one may be particularly interested in: for instance, ordinary crop plants alone; ordinary crop plants and those often called "salt-tolerant" (*i.e.,* hyperplectic); true halophytes; all vegetation.

Being an integrator of soil conditions, a plant cannot distinguish between high OH-ion concentrations and high salinity. The physico-chemical state evoked or elicited by high pH or high salinity (low pC) or both together is expressed by pL, which reflects variations in pH and pC in the same sense as the ions and their total physical effects affect the plant.

An outline of the pH/pL "spectrum" shows how the plant-physiological effects of salinity will vary with edaphic pH, and conversely (Fig. 1).

Unification of Theory of Preservation of Foods

From the growing of organisms to their non-growing is a very short step. It is a step which takes one beyond the pC or osmotic-pressure limits of a pL-spectrum as given above; and indeed to formulate a comprehensive theory of those methods of food-preservation which depend on physico-chemical actions to suppress the activities of micro-organisms by rendering them dormant, is merely to consider the spectrum from the outside, as it were, and to assume that the "wilting-point" of micro-organisms (that is, the point at which they are unable to extract water by physical means from their liquid environment) is not very different from that of higher plants. For introductory purposes, the magnitude of the critical pC or osmotic pressure need not be known; it is sufficient to presume that the conjoint effects of pH, salt- and acid-concentration, and concentration of non-electrolytes, shall express themselves in a "wilting-point" at which spoilage micro-organisms cannot reproduce, owing to reduction of the free energy of water so that the material "keeps" for a long period.

It is therefore practical to collocate all methods of food-preservation in a simple scheme.

From the following indicative outline, purely chemical methods of preserving food have been omitted, and annotation has been reduced to a minimum. It is, for example, known that canned foods are often not sterile. M = micro-organisms.

Group O: M absent: aseptically-drawn sterile fluids.

Group IA(i): M initially present, but removed by filtration or other mechanical means, leaving substrate intact: commercial bottled non-alcoholic fruit juice.

IA(ii): M initially present but removed, or induced to remove themselves, after consuming substantially the whole of a principal substrate: wine, cask beer.

Group IB: M initially present but killed or inactivated by high temperature (in principle; sometimes with other factors assisting, such as absence of much air or presence of an anti-sporulating agent): sterilized fresh milk, evaporated unsweetened milk, "pasteurized beer,"[1] canned meat and vegetables.

[1] The term "pasteurization" is a misnomer as applied to beer. The process of "pasteurization" of beer is distinct from pasteurization of milk (a short-term method of preservation not here considered) and is really sterilization.

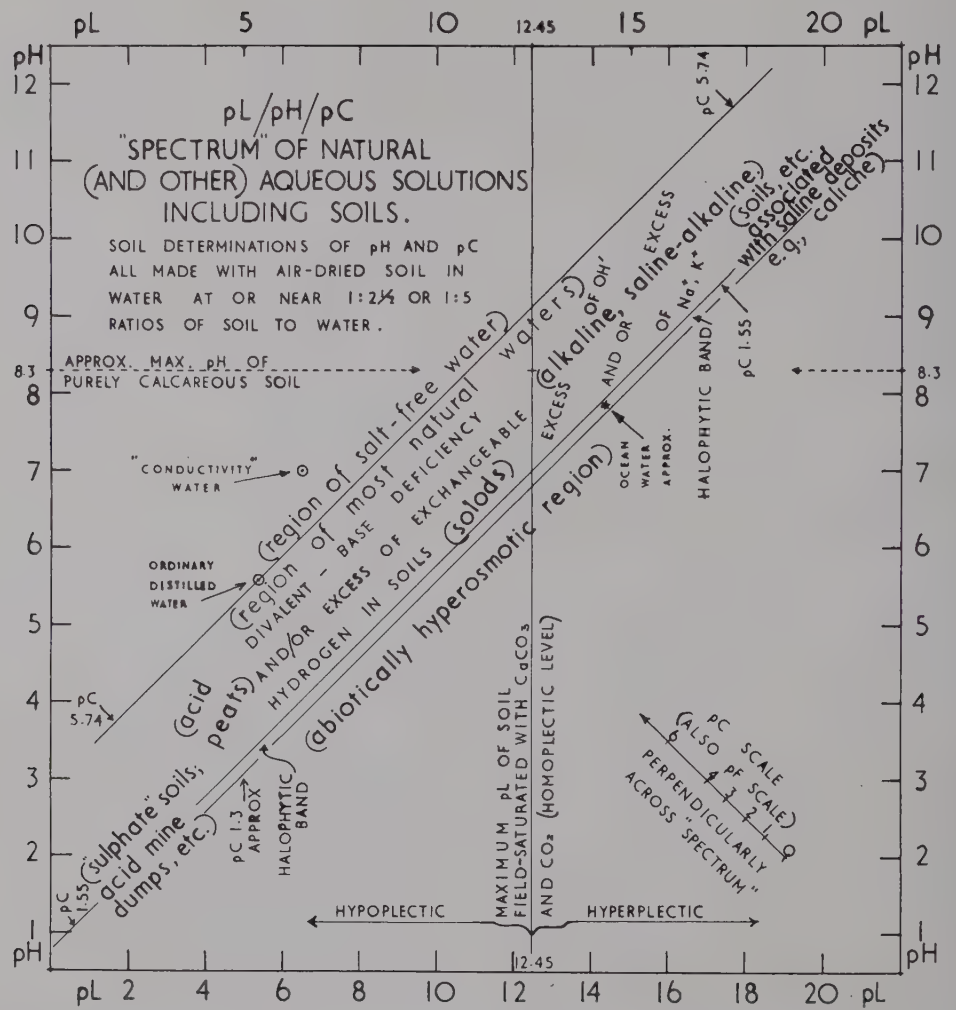

pL/pH/pC
"SPECTRUM" OF NATURAL
(AND OTHER) AQUEOUS SOLUTIONS
INCLUDING SOILS.
SOIL DETERMINATIONS OF pH AND pC
ALL MADE WITH AIR-DRIED SOIL IN
WATER AT OR NEAR 1:2½ OR 1:5
RATIOS OF SOIL TO WATER.
APPROX. MAX. pH OF PURELY CALCAREOUS SOIL
"CONDUCTIVITY" WATER
ORDINARY DISTILLED WATER
(region of salt-free waters)
(region of most natural waters)
DIVALENT - BASE DEFICIENCY AND/OR EXCESS OF EXCHANGEABLE HYDROGEN IN SOILS (solods)
(acid peats)
(abiotically hyperosmotic region)
EXCESS OF OH' AND OR EXCESS OF Na+; K+ (alkaline, saline-alkaline) (soils, etc. associated with saline deposits e.g., caliche)
OCEAN WATER APPROX.
HALOPHYTIC BAND
pC 5.74
pC 1.55
pC 1.3 APPROX
HALOPHYTIC BAND
"sulphate" soils; acid mine dumps, etc.)
MAXIMUM pL OF SOIL FIELD-SATURATED WITH CaCO3 AND CO2 (HOMOPLECTIC LEVEL)
pC SCALE (ALSO pF SCALE) PERPENDICULARLY ACROSS "SPECTRUM"
HYPOPLECTIC
HYPERPLECTIC
12.45
pH
pL

FIG. 1. General classification of soil horizons and natural waters in terms of pL/pH and pH/pC.

The principal band or "spectrum" shown is that which comprises all normal land waters and ordinary crop plants (pC-tolerance between the extreme limits of 5.74 and 1.55). A supplementary band is given to indicate an extension of tolerance to pC 1.3. In this instance and for the sake of clearness, the width of this supplementary band has here been slightly exaggerated. For purposes of detail classification or for particular ecological descriptions, a less comprehensive pH-range could be surveyed, permitting clear-cut subdivision of bands.

The areas likely to be occupied by some principal soil types are roughly indicated by names in brackets; they can be more extensive than the present, purely introductory, indications suggest. The approximate positions for (undiluted) ocean water, distilled water, and conductivity water, are shown. Areas towards the extreme top left and extreme bottom right of the Figure have no physical meaning; they are included to show co-ordinates only.

Certain groups of materials which may not be soils, or can merge into soils, transgress any limit of pC-tolerance of plants; *e.g.*, acid exudates, saline deposits.

Group II: M present initially, but not removed, and with no necessary bar to access of air-borne M: all other methods of preserving food, including removal of water at relatively low temperatures (as sun-drying, haymaking, preparation of honey), industrial dehydration, freezing, addition of salt, sugar, or acid; also ensilage. In Groups O and I, a principal function of the container is to preserve the food or drink from adventitious contamination. In Group II (excepting silage)—where preservation is effected by reduction of free energy, no container is essential except to preserve a hygroscopic product from access of water. Properly made honey or sweetened condensed milk will "keep" indefinitely after the jar or can is opened—unless the material gains moisture from damp air, or otherwise.

For some products, the preservation lasts only as long as a limiting external factor is maintained. In silage and sauerkraut, the reduction of free energy is not as complete as in other, more typical, materials of Group II, and additional security is obtained by exclusion of oxygen.

Like some other foodstuffs, silage "goes bad" after ex-

posure to air: but primarily because of the access of oxygen—not because of air-borne microbial contaminants. In other materials of Group II, the "going-bad" on exposure to air is not, in general, an effect of oxygen or of additional species of microbes, but is a consequence of an increase of free energy resulting from access of water. In frozen materials for example, the proportion of available water is reduced by the low temperature, and this leads to an increase in concentration of solutes; but when the temperature is raised, the ice melts, water again becomes freely available, and forms a dilute solution in microbial cells and substrate.

For some products, several techniques are combined (as for jams: partial evaporation by heat, and addition of sugar to an acid medium).

In free energy we thus have a common denominator for such ecological applications as growth of crop plants and preservation of food in contact with external microbes. Other applications of the concepts of pH/pC and free energy will suggest themselves. The important thing, I feel, is that these concepts enable soil scientists and ecologists of every kind to release themselves from the limitations resulting from an unbalanced attention devoted mainly to solid phases of soil and other materials, and from taking pH as virtually the only manifestation of the physical state of the aqueous phase.

Summary

Hitherto, pH—often incorrectly understood—has been the commonest expression of the physico-chemical states of soils and other environments; and when (electrical) conductivity has also been measured, it could not be brought to "add up" with pH or related features. Nor have the governing effects of pH and conductivity, jointly with each other and with concentration, been given adequate attention in analyses and discussion referring to equilibrium-systems in which a solid phase is concerned.

As ordinarily measured, pH and conductivity (pC) are each integrals of the ionic states of solutions, and also are resultants of the total ionic interchanges in a solution and between a solution and a labile solid phase. Fresh insight into the behavior of solutions and of organisms is obtained when pH and pC are both taken into account: if necessary, in conjunction with other physico-chemical parameters such as total osmotic pressure.

The expression pL (= 2 pH — pC, provided both are measured under certain prescribed conditions) is characteristic of a soil sample, and affords a means of classifying soils with respect to their physico-chemical state. An edaphic "spectrum" of natural (and other) soils and waters is presented in terms of pH, pC, and pL.

As another development of the pH/pC concept, a comprehensive scheme of the theory of preservation of foods is presented.

References

da Costa, J. V. B. 1938. A critical survey of investigations on the "wilting coefficient" of soils. Jour. Agric. Sci. **28**: 243-245.

Mattson, S., and L. Wiklander. 1940. The laws of soil colloidal behavior: XX1 B. The amphoteric points, the pH and the Donnan equilibrium. Part B. Experimental. Soil Sci. **49**: 135-153.

Nicol, Hugh. 1954. pL: a numerical soil characteristic. Trans. 5th Internatl. Cong. Soil Sci. **3**: 166-170.

Nicol, Hugh, and E. K. Schofield-Palmer. 1952. Some relations between conductivity and acidity in soil suspensions and other solutions. Chem. and Indust., No. **44**: 1080-1081.

Schofield, R. K. 1935. The pF of water in soil. Proc, 3rd Internatl. Cong. Soil Sci. **2**: 37-38.

Whittles, C. L., and E. K. Schofield-Palmer. 1951. On pC, pS and pN as indicating functions of electrical soil conductivity. Jour. Soil Sci. **2**: 243-245.

Wilde, S. A. 1954. Reaction of soils: facts and fallacies. Ecology **35**: 89-92.

Hugh Nicol

Chemistry Department,
The West of Scotland Agricultural College,
Glascow, C.2, Scotland

A COMPARISON OF AIR TEMPERATURE EXTREMES IN TWO TAMARACK SITES[1]

As part of a study on the ecology of the larch sawfly, *Pristiphora erichsonii* (Htg.), temperature records were kept during the summer of 1953 in a bog located near Prince Albert, Saskatchewan (latitude 53° 138′ N). The bog was situated in a depression in sand hills lying north of the North Saskatchewan River. The depression was about 180 acres in extent and had no inlet or outlet streams.

The bog forest consists of a mixed stand of tamarack, *Larix laricina* (Du Roi) K. Koch, and black spruce, *Picea mariana* (Mill.) B.S.P., occupying the drier periphery of the bog and a pure stand of tamarack in the wet centre. The mixed stand had an average height of 23 feet, D.B.H. of 2.4 inches, and density of 2,515 stems per acre (735 tamarack and 1,780 black spruce). The pure tamarack stand had an average height of 24 feet, D.B.H. of 2.6 inches, and density of 1,440 stems per acre.

In the mixed stand the trees were clumped around scattered open areas, whereas the trees in the pure tamarack stand were spaced more evenly. The dense, compact crowns of the spruce, as well as the clumping of the trees, formed a more broken canopy than the open and spreading crowns of the tamarack in the pure stand. The development of leaves on the tamarack in the spring of 1953 was as follows: May 8—first buds breaking; June 15—trees in full foliage; July 16—first noticeable defoliation by the larch sawfly.

The ground vegetation in the mixed stand was dominated by *Ledum groenlandicum* Oeder, which reached a maximum height of 18 inches. In the tamarack stand the dominant ground vegetation was *Carex* spp. on the hummocks with *Caltha palustris* L.; *Menyanthes trifoliata* L. var. *minor* Raf. with other water plants and mosses in the depressions. The ground surface in both areas was hummocky, with depressions one to four feet deeper than the tops of the hummocks. The depressions in the pure tamarack stand contained water throughout

[1] Contribution No. 185, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

the summer but those in the mixed stand dried out after the spring runoff.

Two Short and Mason thermographs, model C21352, were operated in the bog during the summer of 1953. The instruments were checked against a standardized mercury thermometer at the beginning and end of the summer. Each thermograph was kept in a Stevenson screen 4.5 feet above the ground surface. This recorded the air temperatures in the trunk space of the forest, defined by Geiger (1950) as the space in a forest stand lying between the ground vegetation and the lower limits of the tree crowns. One thermograph was located in the mixed stand and the other 655 feet distant in the pure tamarack stand. The ground sloped 0.23 per cent between the two thermographs with the mixed stand at the higher level. The instrument shelter in the mixed stand stood in an opening, about five feet north of a clump of tamarack and spruce. The shelter was shaded by spruce and tamarack foliage except in the early morning. In the pure stand the shelter was four feet north of the nearest tree. Except in early morning, the shelter was partially shaded by tamarack foliage.

Results and Discussion

The temperature records from the two thermographs were remarkably similar, but consistent differences in the extremes occurred. Dr. W. G. Wellington, Forest Biology Laboratory, Victoria, British Columbia, suggested that these differences might be significant. The differences varied during the season in a manner apparently related to the foliation of tamarack in the spring and the partial defoliation of this species in late July by the larch sawfly. On the basis of differences in the temperature extremes the season was divided into four periods; April 15 to May 20, May 21 to June 15, June 16 to July 19, and July 20 to September 6. When these periods are compared with the records of tamarack foliation and defoliation the following relationship appears:

April 15-May 20
Tamarack leafless or in bud-opening stage.
May 21-June 15
Tamarack partially foliated.
June 16-July 19
Tamarack in full foliage.
July 20-September 6
Tamarack partially defoliated.
25-50% in the pure stand
50-75% in the mixed stand

Table I gives the mean maximum and mean minimum temperatures for each period during the season. In addition, each day and night was classified on the basis of sky cover as clear, part cloudy, or cloudy and the mean maxima and mean minima for each sky cover class was calculated. This classification was made from the hourly observations taken at the Prince Albert Airport by the Meteorological Division, Department of Transport, Canada. The table shows that in the periods April 15-May 20 and May 21-June 15, when the tamarack was leafless or in the process of putting out foliage, the pure tamarack plot was warmer than the mixed plot. The bare or partially foliated branches of the tamarack appear to have allowed a greater amount of radiant heat to reach the ground, thus accounting for the higher maxima in the pure stand. But these bare branches should also have allowed greater radiant heat loss at night and consequently lower minima. The warmer night temperatures in the pure stand may have been due to a greater amount of wind movement through the trunk space of this open, leafless stand. In the shelter of the clumps of spruce in the mixed stand, temperature inversions would be more likely to form and lower temperatures result.

Table I. *Mean maxima and minima for a pure and a mixed tamarack stand (° Fahrenheit) near Prince Albert, Saskatchewan*

Dates	Sky cover type	No. days	Mean maxima		No. nights	Mean minima	
			Mixed	Pure		Mixed	Pure
April 15-May 20	Clear	13	61	62	16	25	25
	Part Cloudy	10	44	45	8	31	31
	Cloudy	13	52	52	12	28	29
	Total	36	53	54	36	28	28
May 21-June 15	Clear	6	66	68	10	35	37
	Part Cloudy	13	66	68	8	43	44
	Cloudy	7	62	64	8	46	48
	Total	26	65	67	26	41	43
June 16-July 19	Clear	9	74	73	12	46	45
	Part Cloudy	15	73	71	10	45	45
	Cloudy	10	58	58	12	48	47
	Total	34	69	68	34	47	46
July 20-Sept. 6	Clear	12	80	79	23	46	44
	Part Cloudy	16	70	70	10	50	47
	Cloudy	13	63	63	12	52	51
	Total	41	71	71	45	48	46

During the period May 21 to June 15, the angle of the sun's rays was more vertical than in the earlier period and the greater radiant heating would accentuate the differences in the maxima between the pure and mixed stands.

From June 16 to July 19, when the tamarack was in full foliage, the maximum and minimum temperatures in the mixed stand were higher than in the pure stand. The broken canopy of the mixed stand appears to have allowed more radiant heating of the ground during the day than the more solid canopy of the tamarack in full foliage. The lower temperatures in the pure tamarack stand could have been due to the formation of a "cold lake" in the low centre of the bog occupied by the pure tamarack stand. Drainage of cold air down slope from the mixed stand would tend to keep the mixed stand slightly warmer although the similarity of differences in mean minimum temperatures for clear and for cloudy nights suggests that cold-air drainage is not well developed.

After July 20, no difference in the mean maxima occurred, possibly due to the partial defoliation of the tamarack. The decline in the angle of the sun's rays from the previous period may have been a contributing factor by reducing the amount of radiant heating, particularly through the deeper, denser spruce crowns. The mean minima after July 20 were 2° F. higher in the mixed stand than in the pure stand. As this difference is less marked on cloudy than on clear or part cloudy nights, it seems that the partial defoliation of the tamarack opened the pure stand more than the mixed stand and allowed more heat loss due to re-radiation during the nights.

Summary

Differences in the maximum and minimum temperatures recorded during the summer of 1953 between a stand of pure tamarack and an adjacent mixed stand of tamarack and black spruce could be attributed to differences in the foliage and crown characteristics of the two species. From April 15 to June 15, before the deciduous tamarack came into full foliage, mean maximum temperatures were one to two degrees higher in the pure tamarack stand. From June 16 to July 19, when the tamarack was in full foliage, maxima in the mixed stand averaged one degree higher. After July 20, when the tamarack was partially defoliated by the larch sawfly, no differences in the mean maxima occurred.

The mean minima were the same in the two stands for the period April 15 to May 20, when tamarack was leafless or in the early stages of foliation. From May 21 to June 15, with the tamarack partially foliated, the mean minimum in the pure stand was two degrees higher than in the mixed stand. While the tamarack was in full foliage and after partial defoliation by the larch sawfly, the mean minimum of the pure stand was 1-2° F. lower than in the mixed stand.

Reference

Geiger, R. 1950. The climate near the ground. Cambridge, Mass.: Harvard.

W. J. Turnock[2]

Forest Biology Laboratory,
Canada Department of Agriculture,
Winnipeg, Canada

[2] Agricultural Research Officer

EFFICIENCY OF FINELY-DIVIDED VS. TAPE-LIKE AQUATIC PLANT LEAVES

The assumption that plants with finely divided leaves have an advantage in absorption of nutrients from the environment over those with broad, flat leaves is fairly common. So also is the assumption that the finely divided leaf is best-suited to small ponds and quiet waters, while broad, flat leaves are particularly well-adapted to running water; see Romell (1927), for example. In the western end of Lake Erie, plants with these two radically different leaf types, *Myriophyllum exalbescens* Fernald and *Vallisneria americana* Michx., are predominant rooted plants and are found growing together. Apparently water action (or lack of action) is tolerated equally well by both.

Uspenskij, as quoted by Arber (1920), using *Potamogeton perfoliatus* and *Myriophyllum spicatum*, worked out the ratio of surface to volume for the broad, flat leaf type and the finely divided one and concluded that both types were fairly equal in efficiency.

The present paper is the result of a comparative study undertaken in August, 1954, at the Franz Theodore Stone Institute of Hydrobiology, using *Myriophyllum exalbescens* and *Vallisneria americana*. The study includes determination of rate of photosynthesis in μ moles/gm./hr. and ratio of area to weight for both plants. Experiments were performed between 9:00 and 11:00 a.m., August 2-18, inclusive. The problem was suggested by Dr. J. Verduin.

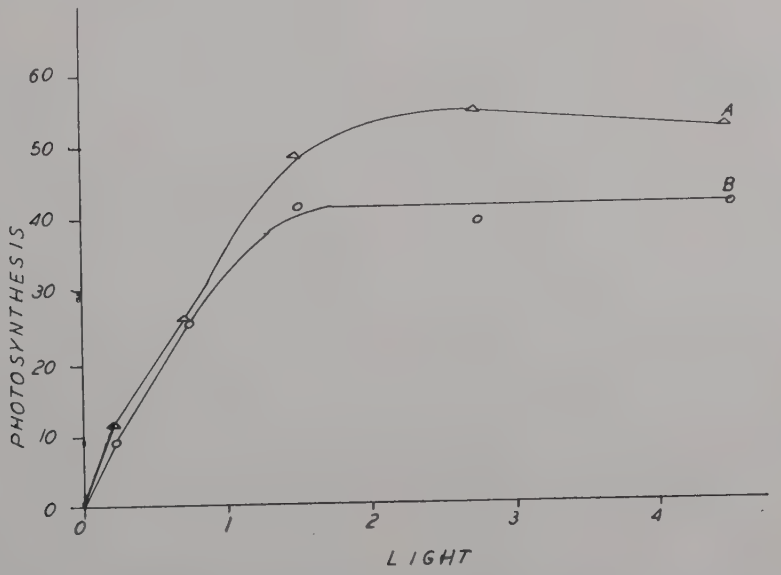


Fig. 1. Photosynthesis (μ moles CO_2/gm./hr.) in *Myriophyllum* (A) and *Vallisneria* (B) plotted against light intensity in milliamperes. Each curve represents 9 experiments.

Experimental Procedure

Myriophyllum tips 10 cm. long, weighing about 0.6 gm. and 30 cm. leaf portions of *Vallisneria*, weighing about 0.4 gm., were inserted into 250-ml. bottles of lake water at 0.5 m. intervals from surface to 1.5 m. depth. Light intensity was measured in milliamperes at each depth by use of a submarine photometer to permit comparison of different experiments at similar light intensities. At the end of an hour, the bottles were removed from the lake and the pH difference between the black and clear bottles was determined by use of a Beckman pH meter. The CO_2 change (rate of photosynthesis) was calculated, using a graph constructed by making step-wise titrations and pH determinations using weak sodium hydroxide (0.01 N).

The area of the tape-like *Vallisneria* leaves was easily computed by simply multiplying length by width by 2 (to account for both sides). In measuring the area of *Myriophyllum*, the leaves were removed from the stem and the area computed by multiplying the total length of leaflets per leaf ($\times \pi$) by their diameter (mean of 5 measurements per leaflet) under the 100 $\times$ magnification of a compound microscope. The area of the midrib of each leaf was computed the same way. Fresh weight of the plants used in each experiment was obtained by blotting off excess water and weighing on a balance, having a sensitivity of 0.1 gm.

Results and Discussion

Figure 1 shows the micromoles/gm./hr. plotted against light intensity. Each curve is a composite of 9 experiments. The day to day variation was such that the highest values under optimum light were about 2.5 times the lowest. The curves are essentially similar; the optimum light for both plants falling between 1.6 and 4.5 milliamperes, with hourly rate per gram at optimal light for *Myriophyllum* amounting to 54 and for *Vallisneria* amounting to 41 micromoles. The *Myriophyllum* rate is 1.3 times the *Vallisneria* rate. The ratio of surface to weight in the two plants was 88 cm.^{2}/gm. for *Vallisneria* and 89 cm.^{2}/gm. for *Myriophyllum*, indicating that the CO_2-absorbing surface per unit weight was practically identical.

Romell's assumption that the finely divided leaf is best adapted to quiet water and the broad, flat type is adapted to running water, appears to be untenable for these two plants in this particular area. Confirmation is given to Uspenskij's conclusion that the dissected and flat types of leaf are practically equal in efficiency. Arber states (p. 139-140) that Uspenskij, "admits that, apart from the actual ratio of surface to volume, the dissected leaf may possibly have an advantage over the corresponding flat leaf, in tapping a greater volume of the medium; he thinks, however, that though this factor would be of importance in absolutely still water, its significance is much reduced if, as is nearly always the case, movement has to be taken into account." Perhaps the slightly higher rate in *Myriophyllum* may be attributed to such a "tapping of greater volume" in the quiet water within the bottles.

References

Arber, Agnes. 1920. Water plants. Cambridge Univ. Press, London.

Romell, Lars-Gunnar. 1927. Flora 121: 125-156.

E. Eloise Whitwer

Department of Biology,
Bowling Green State University,
Bowling Green, Ohio

ECOLOGY OF THE BEAN CLAM *DONAX GOULDI* ON THE COAST OF SOUTHERN CALIFORNIA[1]

During the past seventeen years the writer has examined at frequent intervals the successive populations of this little bivalve on the beach near the Scripps Institution and elsewhere. The times of arrival on the beach, the nature of the food, the rates of growth at various ages and seasons, the parasites, the maximum life-span, the arrival in certain years of almost incredible numbers and the sudden disappearance of these resurgent populations within two to three years, including both old and young individuals, have been the subjects of careful investigation.

Inspection of Fig. 1 will show that during the present century these resurgent populations have appeared on the beach at La Jolla at irregular and unpredictable intervals varying from two to fourteen years.

It is well known that other species of this genus in various parts of the world are likewise almost completely exterminated at intervals by the sudden death of apparently vigorous populations (Pelseneer 1928). It is only recently, however, that a satisfactory explanation for this unusual behavior of an animal population has been found and certain details of the problem remain to be elucidated. Coe (1953) has reported finding a minute unicellular organism in the tissues and cavities of the moribund individuals and these organisms were considered to be the causative agent of the deaths. Fitch (1953) mentioned such resurgent populations and their sudden disappearance.

Donax gouldi Dall is normally biennial on this part of the coast, although in certain years nearly all individuals have died after spawning when only one to one and one-half years old. In other years most individuals survive this first spawning period and die after spawning again in their second summer. There are also a few exceptional individuals which retain their vigor until they have completed a third spawning period in the spring or early summer of their third year. Most of the deaths have occurred during the warmest part of the year, that is, from June to September. Excessive numbers of dinoflagellates may sometimes contribute to the mortality.

The resurgent populations mentioned have been recorded at La Jolla in 1894-95, 1909-10, 1913-15, 1931-32, 1934, 1937-38 and 1949-52 (Coe 1953) and have doubtless occurred in earlier years (Fig. 1). In the resurgence of 1937-38 there were at least 10,000 clams per square meter in some areas in the intertidal zone, while the numbers in the 1949-52 resurgence averaged more than 20,000 per square meter in an irregular band 2 to 5 meters wide which extended with some interruptions for more than five miles along the beach. In addition to this

[1] Contributions from the Scripps Institution of Oceanography, of the University of California. New Series, No. 621.

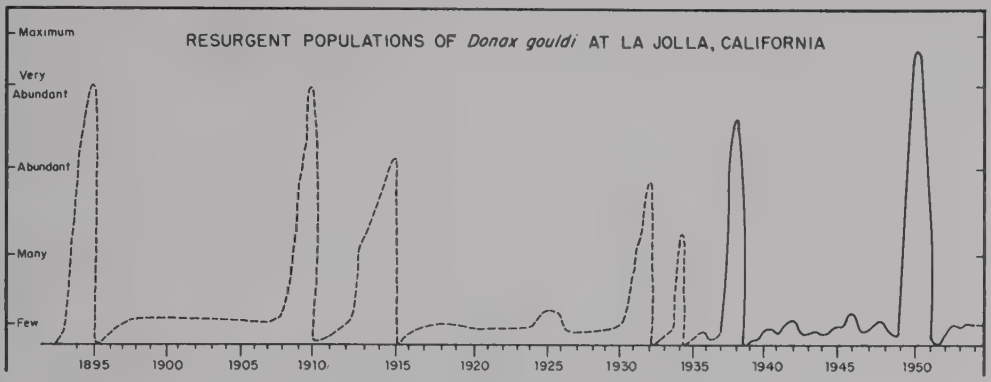


FIG. 1. Resurgent populations of *Donax gouldi* in the intertidal zone at La Jolla, California. Estimated relative abundance: "few," less than 5 per square meter; "many," 5 to 20; "abundant," more than 100; "very abundant," more than 1000; "maximum," more than 10,000 per square meter. The populations in the years preceding 1926 and from 1928 to 1936 (dashed line) are estimated from the incomplete records by Dr. W. E. Ritter, Mr. Percy Barnhart and others; those of 1926, 1927, 1937 and subsequent years from personal observations by the writer (solid line).

immense number in the intertidal zone, scattered individuals were found as far as 200 meters from the shore in water up to 6 meters in depth. In the immediately preceding year the numbers did not exceed one clam per square meter in the same locality. Precise data for the other resurgent populations reported are not available but the records indicate that they were similar, since large quantities were gathered for broth and poultry feed and in 1938 Donax clam broth was canned commercially at one locality.

After one to three years the populations have disappeared so completely that less than a dozen individuals have been found in an area occupied by millions a few months previously. The deaths have included not only the older members of the population but also the younger individuals which have arrived since the resurgence began. The history of one of these resurgent populations has been reported by Coe (1953) in this journal.

It has been mentioned that the life span of Donax in this locality is seldom more than two, or occasionally three, years and that fact might help to explain the deaths of the older members of the resurgent group but not those of all the younger individuals which settled on the beach subsequently. Examination of the moribund clams, both old and young, showed that their tissues were soft and slightly greenish in color, usually containing vast numbers of minute unicellular organisms. These organisms were found in the enlarged blood spaces and connective tissues, as well as within the phagocytes, within the cells of the digestive diverticulum, epithelium of gut, and in other organs.

Each of these parasitic organisms was found to be an irregularly spherical or ovoid cell, 2 to 6 μ in diameter and apparently similar to *Dermocystidium marinum* Mackin, Owen, and Collier, which causes so much destruction of oysters in the Gulf of Mexico and elsewhere along the southeast coast of the United States (Mackin 1951). As is also the case with the oyster disease, the disastrous effects of these parasites in Donax are evident mainly during the warmer months of the year.

Since the resurgent population may appear in a locality which was occupied by only a few individuals during several preceding years, it is concluded that vast swarms of larvae must have arrived from some other locality with a large breeding population. With a larval life of presumably two to three weeks or more, the free-swimming larvae may be carried for many miles by the ocean currents which on this coast have an average velocity of four to five miles a day. It may be assumed that the larvae reached the beach at the precise time when they were ready to metamorphose and settle in the sand. Preceding the arrival of the larvae at La Jolla it is known that there were spawning populations on beaches both north and south of that locality.

The young clams are first found in a broad band near the middle of the intertidal zone on a sandy coast fully exposed to the surf of the ocean. There they remain near the surface of the sand with their siphons projecting into the water whenever the sand is covered by water. They are later scattered widely by the action of the surf, principally to lower levels, and some are carried into water beyond the low-tide limit. The positions of the clams beneath the surface of the sand can often be detected by the projecting tufts of the hydroid Clytia.

Food. Whenever the clams are covered by water, they feed on particles of organic matter in suspension. These include small diatoms, dinoflagellates, bacteria, minute ova of invertebrates, spermatozoa, and a large proportion of detritus derived from the disintegration of animal and plant cells (Coe 1948).

Spawning. The first spawning commonly takes place at the age of about one year, or one and a half years for those hatched late in the season. The spawning season for the populations at La Jolla extends from April to October or November or six to seven months. Each female produces 1,000 to 50,000 or more yellowish ova at each ovulation and several ovulations may occur in the same year. Because of the extended spawning season, the average age of any year-class may be reckoned from the middle of July (Fig. 2). The young settle on the beach in greatest numbers from July to September.

Rates of growth. Increase in size is less rapid than in some other species, for the young clams average only about 12 mm. in length at the age of one year and 18 mm. at the age of two years. Most individuals on this beach have died after spawning during their second year.

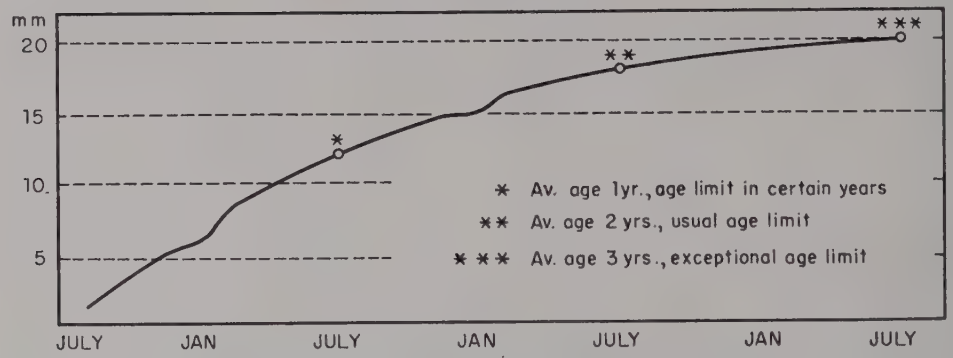


FIG. 2. Average rates of growth of *Donax gouldi* at La Jolla. Individuals which set on the beach in early July reached an average length of 12 mm. when one year of age and 18 mm. at the age of two years. The relatively few survivors were about 20 mm. long when they all died near the end of their third year.

The survivors average about 20 mm. in length at the extreme age of three years. Shells more than 24 mm. long are seldom found in this locality and in certain years the maximum size of spawning individuals is only 12-16 mm.

Enemies. Gulls devour vast numbers of Donax of all sizes and regurgitate the empty shells. The clams are eaten also by rays and by several species of fishes, notably corvina and the surf perches. These fishes frequently bite off and devour the siphons of the clams instead of taking their whole bodies.

Parasites. Many of the clams, and in some areas most of them, are infested with trematodes, particularly *Postmonorchis donacis* Young (1953). The parasites are first found in the visceral mass of the body and when present in large numbers encroach upon the gonads to such an extent as to render the clam more or less completely sterile but without apparent loss of vigor. The parasites evidently absorb the nutrition which would otherwise be available for the development of the gametes. The young parasites enter the connective tissue of the visceral mass and become sporocysts. These increase in size and produce the tailed cercariae. The latter give rise to the metacercariae which later encyst at the base of the siphons and edges of the mantle, as well as in the gills. The adults presumably live in the rectum of fishes (Young 1953).

A far more injurious parasite is the minute unicellular organism which sometimes contributes to the death of the entire local population, as mentioned in a preceding paragraph.

SUMMARY

This paper summarizes the results of observations during seventeen years on the habits and habitat, food, rates of growth at different ages and seasons, periods and conditions of spawning, enemies, and parasites. Data relative to the seven resurgent populations which have appeared on that beach in the past sixty years are included. In the resurgence of 1949 the population changed from an average of less than one clam per square meter to more than 20,000 within two months. An epidemic disease soon developed and the mortality became so great that within three years less than a dozen individuals, old or young, could be found in an area formerly occupied by millions. A minute unicellular organism was apparently responsible.

REFERENCES

Coe, W. R. 1948. Nutrition, environmental conditions, and growth of marine bivalve mollusks. J. Mar. Res., **7**: 586-601.

Coe, W. R. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. Ecology, **34**: 225-229.

Fitch, J. E. 1953. Common marine bivalves of California. Calif. Dept. Fish and Game, Fish. Bull. No. 90: 1-102.

Mackin, J. G. 1951. Histopathology of infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum* Mackin, Owen, and Collier. Bull. Mar. Sci. Gulf and Carib., **1**: 72-87.

Pelseneer, P. 1928. Les parasites des mollusques et les mollusques parasites. Bull. Soc. Zool. France, **53**: 158-189.

Young, R. T. 1953. *Postmonorchis donacis*, a new species of monorchid trematode from the Pacific coast, and its life history. J. Washington Acad. Sci., **43**: 88-93.

WESLEY R. COE
SCRIPPS INSTITUTION OF OCEANOGRAPHY,
LA JOLLA, CALIFORNIA

VEGETATION AND THE ALIGNMENT OF ENVIRONMENTAL FORCES

Yet another general interpretation of climax vegetation in terms of the alignment of environmental forces has recently been proposed in a preliminary note to Ecology (Dansereau 1954). The processes of vegetation development are envisaged as dependent upon a relay of factors, with successive release from edaphic to biotic and finally to climatic control, and with all seres theoretically convergent upon the climax.

To the present writer, such an interpretation seems unlikely to be of general validity. Inasmuch as spatial variation or temporal change in soil, biota, topography, or climate may effect differences or changes at any stage

of succession, the complexity of pattern and process in both vegetation and soil is clearly a reflection of the *continual* interaction of several partially independent ecosystem factors (Jenny 1941, Major 1951, Crocker 1952, Billings 1952).

Edaphic differences—such as those between limestone drift, non-calcareous clay, and sterile sand—will certainly have a selective effect on pioneer plants, but will also be of extremely great importance for their successors. Moreover, there is little reason to believe that differences in soil parent material can always be overcome to the extent that they cease to influence plant distribution (Beadle 1951). Nor can rhythms and extremes of climatic factors —moisture, temperature and light—ever fail to affect vegetation at all stages of its development, including the germination and establishment of the very first colonizing disseminules. Topography may likewise condition entire plant successions—through its effects on drainage, leaching, aggrading and degrading surfaces, microclimate and biotic isolation. Lastly, the availability of disseminules, and their tolerances, will directly determine pioneer floras no less than succeeding ones. Differences in powers of dispersal must have been of extreme importance just after the retreat of the great ice sheets, and are still of fundamental significance for vegetation patterns today (Harrison 1951). To such an extent, the biotic factor is involved in the very earliest stages of vegetation formation, although it is of course a truism that in the course of succession, organisms become ever more important in determining the nature of the environment itself.

Since all the above factors are operative everywhere and at all times, we may conclude that regional and temporal alignments of environmental controls are of necessity inter-related, and depend upon how effectively each ecosystem factor varies in both space and time. In this connection, the possibility of factor compensation must always be borne in mind (Billings 1952). Single factors may undoubtedly control plant distribution over limited areas, within which variation of other factors is insufficient to influence any of the floristic elements. However, the multi-factorial hypothesis referred to above would appear to allow a clearer interpretation of such cases than the rather artificial concept of a theoretical climatic climax, inhibited in certain circumstances by topographic, edaphic, or biotic factors.

The above arguments can best be considered with reference to particular cases, and most ecologists will no doubt wish to test their validity for areas with which they are familiar. Here it may suffice to examine briefly the situation in northern Britain—so ably described by Pearsall (1950)—in relation to Dansereau's views.

According to Dansereau, soil parent material exerts a strong selection upon pioneer plants, which must endure physico-chemical adversity. Hence, high tolerance and low requirements prevail in early stages of succession, under edaphic dominance. In contrast, the climax is said to exhibit high requirements and low tolerance, with efficient utilization of a rich environment under climatic control. However, in northern Britain, postglacial soil development has probably involved floristic restriction, through depletion of plant nutrients and drainage impedance. In both wet and dry sites, it is unlikely that the original glacial drift, rich in easily soluble plant nutrients, exerted more physico-chemical selection upon the pioneer flora than upon present vegetation, though it must have been different in kind. Soil texture was of course very different, and available nitrogen may have been scarce, although a good deal may be supplied from the atmosphere. However, the vegetation of today is strongly conditioned by edaphic factors, in that leaching and drainage impedance must have gradually ousted more demanding species from large areas colonized in early postglacial times. Many such plants are now confined to flushed or unstable soils (Godwin 1949). Thus, it can scarcely be maintained that the climax vegetation in northern Britain exploits a rich environment as regards nutrients, though it may tolerate (or require) high moisture. It may even be doubted whether the standing crop of vegetation has increased since the establishment of a closed cover. The hypothesis of ultimate climatic dominance also fails in this region, for Pearsall (1950) has abundantly demonstrated that variations in each ecosystem factor are of very great importance in determining vegetation pattern and development.

References

Beadle, N. C. 1951. The misuse of climate as an indicator of vegetation and soils. Ecology **32**: 343-345.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. **27**: 251-265.

Crocker, R. L. 1952. Soil genesis and the pedogenic factors. Quart. Rev. Biol. **27**: 139-168.

Dansereau, P. 1954. Climax vegetation and the regional shift of controls. Ecology **35**: 575-579.

Godwin, H. 1949. The spreading of the British flora considered in relation to conditions of the late-glacial period. Jour. Ecology **37**: 140-147.

Harrison, J. H. 1951. Fresh aspects of Irish vegetational problems: I and II. Irish Naturalists Jour. **10**: 125-130 and 145-149.

Jenny, H. 1941. Factors of soil formation. McGraw-Hill Book Co., New York and London.

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology **32**: 392-412.

Pearsall, W. H. 1950. Mountains and moorlands. Collins, London.

Eville Gorham

Freshwater Biological Association,
The Ferry House, Far Sawrey,
Ambleside, Westmorland,
England

OCCURRENCE AND ECOLOGY OF THE HYDROID *BIMERIA FRANCISCANA* IN LAKE PONTCHARTRAIN, LOUISIANA[1, 2]

In conjunction with the current ecological survey of Lake Pontchartrain in Louisiana, the junior author has encountered large quantities of a single species of hydroid. Although major attention of the survey has been devoted to commercially important fishes and invertebrates, field notes on relative abundance and ecology of this hydroid have been kept throughout the year. Preserved and living material have been shipped to the senior author, and cultures prepared from the latter form the basis for the laboratory observations reported herein. The hydroid is identified as *Bimeria franciscana* Torrey.

Identification and Description

This species was originally described by Torrey (1902) from several collections made in San Francisco Bay, California. It has been reported from India by Leloup (1932). Fraser (1944) did not record this species from the Atlantic coast but established the name *B. tunicata* for specimens from Louisiana. Specimens taken by Frey (1946) from oyster beds in the Potomac River were also identified by Fraser (1945) as *Bimeria tunicata*. Deevey (1950), comparing large collections from Texas and Louisiana with extensive ones from San Francisco Bay, was unable to find any characteristic differences. A careful reading of Fraser's descriptions also fails to disclose any sharp distinction between the two species. Since our specimens correspond satisfactorily with Torrey's original description and with Fraser's descriptions of both species, we follow Deevey in regarding *B. tunicata* as a synonym for *B. franciscana*.

The following description parallels those of Torrey (1902) and Fraser (1937, 1943, and 1944) and is correct for our specimens.

Bimeria franciscana Torrey

Trophosome. Colonies in clusters with a height up to 9 cm. The main stem is distinct and smooth, lacking nodes or annulations. It has a heavy, brown perisarc. Branches vary in length and in relation to the main stem; their bases are conspicuously annulated. Secondary branches are uncommon, and when present support only a few hydranths. The hydranths are on short pedicels which are annulated basally but become somewhat rugose at the base of the hydranths. The hydranth bears a single whorl of filiform tentacles. Large hydranths have up to 16 tentacles but smaller ones may have as few as 9 or 10. Hypostome conical. The stolons sometimes form a dense network of tubes with much interlacing and some anastomosis (discussed below). They may grow over the bases of older stems for several millimeters.

Gonosome. Small globular sporosacs on short pedicels arise near the base of hydranths. They have a perisarcal investment.

Distribution and Ecology

Distribution records for the hydroid are based upon direct observation and beach seine collections from shallow water and trawl collections from deeper water. During the survey *B. franciscana* has been taken from

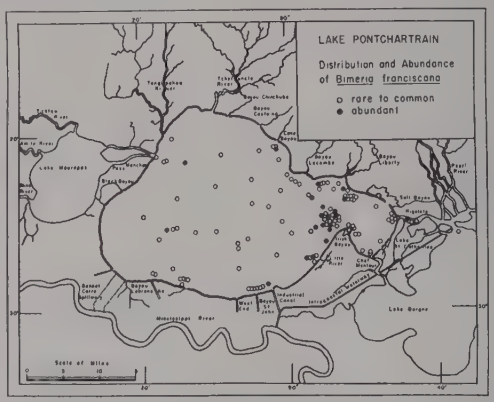


Fig. 1. Map of Lake Pontchartrain showing distribution and abundance of *Bimeria franciscana*.

almost all parts of Lake Pontchartrain (see Fig. 1) although abundance has been found to vary considerably from one locality to another. The areas of least density appear to be the central and western portions of the lake where the hydroid appears to be widespread but in low concentrations both near the shore and in deeper waters. Many of the records of its presence in this area were based upon very small quantities and were reported as "rare" in the field notes. This apparent paucity in the central and western sectors is not due entirely to lack of collecting since over 200 of the approximately 500 collections made from the lake have been taken from these areas. The one record of abundance in a collection from the southwestern quarter of the lake referred to a log carpeted with the hydroid which was brought up by a trawl early in the survey.

In one collection made about 3½ miles east of Pass Manchac the hydroid was quite abundant, and its quantity indicated the probable presence of a heavy concentration in the specific area.

Collections made from the eastern sector of the lake, on the other hand, revealed general widespread distribution as well as several heavy local concentrations of the hydroid. The regions of local abundance appeared to be deep holes, including those created artificially by dredging operations, and shallower waters, particularly in the deltaic areas near the entrances of fresh or salt water. Both of these situations, as well as that reported above near the mouth of Pass Manchac, were characterized by high organic content of the bottom and some current. The area of greatest concentration, however, appeared offshore from Irish Bayou. As will be demonstrated in a later paper, this general area is frequently swept at high tide by a tortuous, shifting river of salt water which passes into the lake through the Rigolets. Considering the above pattern of distribution, it appears probable that among the primary physical factors determining the presence and local abundance of the species, are high organic content of the bottom and the presence of a moderate current to agitate the bottom and distribute the associated microbiota.

B. franciscana is quite euryhaline, and in Lake Pontchartrain a salinity range of 2.5-12.0 $^0/_{00}$ has been noted

[1] Contribution No. 579 from the Department of Zoology, Indiana University.

[2] Field work reported in the present study was supported by the Commercial Seafoods Division of the Louisiana Wildlife and Fisheries Commission.

for the species. Considering its abundance near the mouths of fresh water passes and bayous, it must be able to tolerate fresh water at least for short periods. Since it has been taken in some quantity from the Rigolets and Lake Borgne it must also tolerate temporary exposure to salinities higher than those indicated. In the Potomac River the habitat of the species is characterized by a salinity range of 3.0-15.0 $^0/_{00}$ (Frey 1946) which agrees well with the observations in Lake Pontchartrain. Regardless of the total observed range of tolerance, the species appeared to be most luxuriant in areas where the salinity varied around 4.0-6.0 $^0/_{00}$.

Cultures have been grown successfully on glass slides in small dishes with daily feeding of newly hatched brine shrimp (*Artemia*). Specimens were kept for four months in 1/10 sea water (salinity 3.5 $^0/_{00}$) and in 1/3 sea water (11.7 $^0/_{00}$). Both such cultures grew well and served as a source for subcultures. A colony kept in sea water (35.0 $^0/_{00}$) for three weeks showed good growth.

A colony placed in sea water diluted to a salinity of only 1.0 $^0/_{00}$ appeared at first to suffer somewhat: tentacles were shortened, there was a cessation of circulation in the stolons, growing tips retracted, and feeding movements of the hypostome were slow. After three days, however, the colony was still able to feed, there was circulation in some of the stolons, and some new growth. From this it appears that 1.0 $^0/_{00}$ is about the minimum salinity which can be tolerated.

When specimens were placed in pond water the hydranths regressed within two days. However, when returned to 1/3 sea water new hydranths developed. This result confirms the supposition based upon field observations that its abundance near the mouths of fresh water passes and bayous indicates tolerance for short exposures to fresh water.

During the summer when water temperatures reached 34.0°C., the hydroid achieved its most luxuriant growth. In the winter, however, when the water temperature dropped to 9.0°C., the hydranths regressed completely, and naked stems were present in collections made from January through March.

During August while specimens were growing in the laboratory, the temperature was often above 32°C. However, colonies placed in an incubator at 37.5°C. suffered regression of all hydranths in less than one day. They recovered when restored to room temperature.

Of 14 preserved colonies examined, only four possessed gonophores. Three of these were taken in the easternmost part of Pontchartrain where salinity was higher. It is quite likely that gonophore production is seasonal and depends upon narrower ranges of environmental factors than those permissible for hydroid growth. The facts at hand are inadequate to determine the factors affecting gonophore production.

Bathymetrically, the species has been encountered in Lake Pontchartrain on bottoms from 0 to 60 feet in depth which is in general accord with Fraser's (1937) statement of 0-7 fathoms in San Francisco Bay. Most of the present observations, however, were based on specimens taken from water less than 15 feet in depth. Wide variation in the turbidity of the water of Lake Pontchartrain has been observed, and Secchi disc readings of 1 to 12 feet have been recorded. Turbidity of the water in this shallow lake is determined largely by heavy winds, which may roil the bottom with considerable force.

Deevey (1950) reported *B. franciscana* attached to buoys on the Texas coast. In Lake Pontchartrain, observations have shown that a variety of substrata is utilized for attachment including clam shells, logs, sticks, and upright posts as well as silt and sandy silt bottoms.

Nothing is known of the natural food of the species. In the laboratory, healthy cultures are maintained by regular feeding with *Artemia* larvae.

Growth of Stolons

Colonies maintained on a glass surface in the laboratory send new stolons along the substratum from which new upright hydranths develop. As the pedicel of such a hydranth elongates, it becomes a main upright stem, giving off new hydranths and lateral branches. Stolons of a colony growing in this manner eventually run into other stolons of the same colony and fuse, forming a reticulate stolonic mesh on the substratum.

In most hydroids, the stolons which meet do not anastomose but grow over one another, as has been directly observed in *Cordylophora* and *Campanularia*. Stolonic fusion is especially characteristic of hydroids of the family Hydractinidae which normally live on shells occupied by snails on hermit crabs. Here the stolon system may be a network of anastomosing stolons (*Stylactis*), or stolons may expand to produce a solid mat (*Hydractinia*).

It has been suggested (Teissier 1927; Crowell 1950) that the capacity of stolons to fuse is an adaptive feature enabling the hydroids to live on shells where the surface available for attachment is quite limited, and it is correlated in hydractinids with the production of a dense colony. In hydractinids, all hydranths arise directly from the stolonic mat; there are no stems or branches. Species of *Bimeria* (family Atractylidae) are the only hydroids with upright stems in which this fusion of stolons has been observed. The occurrence of this phenomenon in *Bimeria* indicates it is not an adaptive feature peculiar to hydractinids.

Discussion

Bimeria franciscana possesses demonstrably wide ranges of tolerance for salinity, turbidity, temperature, depth, and substratum; and on the basis of information presented herein, it appears to be one of the most hardy hydroids for which habitat information is available. Its wide distribution in Lake Pontchartrain is of interest since it is one of the few sedentary invertebrates recorded from the harsh environment of the lake. It is apparent that the species is tolerant of sudden and pronounced fluctuation in conditions of the environment. Unfortunately, available data do not permit detailed analysis of seasonal aspects of the life history of the species.

Since *Bimeria franciscana* flourishes in the eastern sector of Lake Pontchartrain where sport fishing is most intense, the species achieves a position of economic significance. This hydroid is often taken in quantity by commercial shrimp fishermen, and it is undoubtedly the source of vehement agitation by sports fisherman contending that trawls are destructive to "weed beds" in the lake. Whatever the overall biological effect may be in disturbance of *Bimeria* beds, this certainly would not amount to removal of basic producers of organic material. Further studies are in progress on the role of this hydroid as a source of food and shelter for other invertebrates and small fishes.

Summary

1. The hydroid *Bimeria franciscana* is found in large quantities in Lake Pontchartrain and is most abundant

in areas characterized by high organic content of the bottom and some current.

2. It tolerates a wide range of salinities from 2.5-12.0 $^0/_{00}$ in the lake and from 1.0-35.0 $^0/_{00}$ in laboratory culture, and it can also survive temporary exposure to fresh water.

3. Seasonal records suggest that best growth occurs in the summer when the water temperature may reach 34.0°C. In the laboratory, it underwent regression at 37.5°C. but was not killed.

4. Young growing stolons are characterized by the ability to anastomose with others, a feature which otherwise is known to occur in hydroids of only one family, the Hydractinidae.

5. Quantities of this hydroid, frequently taken in commercial shrimp trawls, have popularly been interpreted as vegetation. Economic effects of disturbance of hydroid beds in the lake are at present unknown.

References

Crowell, Sears. 1950. Individual specificity in the fusion of hydroid stolons and the relationship between stolonic growth and colony form. Anat. Record, **108**: 560-561.

Deevey, E. S. 1950. Hydroids from Louisiana and Texas, with remarks on the Pleistocene Biogeography of the Western Gulf of Mexico. Ecology, **31**: 334-367.

Fraser, C. McL. 1937. Hydroids of the Pacific Coast of Canada and the United States. Univ. Toronto Press.

———. 1943. Distribution records of some hydroids in the collection of the Museum of Comparative Zoology at Harvard College, with descriptions of new genera and new species. Proceedings of the New England Zoological Club, **22**: 75-98.

———. 1944. Hydroids of the Atlantic Coast of North America. Univ. Toronto Press.

———. 1945. Notes on some recently collected hydroids in the United States National Museum with descriptions of three new species. Jour. Washington Acad. Sci., **35**: 21-23.

———. 1946. Distribution and Relationship in American hydroids. Uni. Toronto Press.

Frey, D. G. 1946. Oyster bars of the Potomac River. Special Scientific Report No. 32, Fish and Wildlife Service, U. S. Dept. of the Interior. Washington.

Leloup, E. 1932. Une collection d'hydropolypes appartenant l'Indian Museum de Calcutta. Rec. Ind. Mus., **34**: 131-170.

Teissier, Lise and G. Teissier. 1927. Les principales étupes da développement d'Hydractinia echinata (Flem.). Bull Soc. Zool. France, **52**: 537-547.

Torrey, H. B. 1902. The Hydroida of the Pacific Coast of North America. Univ. of Calif. Pub. Zool., **1**: 1-104.

Sears Crowell

Indiana University,
Bloomington, Indiana

Rezneat M. Darnell

Tulane University,
New Orleans, Louisiana
(Now at Marquette University)

LIGHT AND MYCORRHIZA DEVELOPMENT

Björkman (1942) has proposed a theory that seems to account for the varying degrees of ectotrophic mycorrhiza development occurring under different environmental conditions. He believes, and has obtained strong supporting evidence, that ectotrophic mycorrhiza form when there is a surplus of carbohydrates in the host plant. This theory is in good accord with other aspects of the mycorrhizal problem. Hatch (1935) and others have observed extensive mycorrhizal development under conditions of moderate soil deficiencies of nitrogen, phophorous, potassium, and calcium. Moderate deficiencies of these elements sometimes retard vegetative growth and result in the accumulation of surplus carbohydrates.

By the same reasoning, mycorrhizal development should be directly correlated with the light intensity under which the host plant is growing, providing other environmental conditions permit the accumulation of surplus carbohydrates. Björkman (1949) grew pine and spruce seedlings in the greenhouse under different light intensities, using six forest soils of "extremely varied chemical composition." He found that the frequency of occurrence of mycorrhiza generally followed the curve of carbohydrate production in relation to light intensity found by Stålfelt (1924). Under natural conditions on similar soils, the occurrence of mycorrhiza accordingly should be closely related to the light intensity under which the host plants are growing. A study, therefore, was made in the Duke Forest (North Carolina) to determine if such a relation existed among loblolly pine (*Pinus taeda* L.) seedlings growing under natural conditions.

Procedure

Seedlings were collected in October from within a loblolly pine stand, from a bulldozed area in the open, and from an open area that had not been bulldozed. Bulldozing had stripped off the A horizon and the seedlings were growing on the B horizon of Georgeville silt loam. The soil was the same type and series at the other two locations. Light intensity was measured at noon on a clear day within the pine stand where the seedlings had been taken up, and in the open. The average of several readings within the stand was 31 per cent of full sunlight.

The roots were carefully washed out of the soil after soaking overnight. The number of mycorrhizal tips per centimeter of root length was determined by either (1) measuring total root length and counting all mycorrhizal tips, or (2) counting mycorrhizal tips on randomly selected segments of the whole root. The whole root was used when the root system was small and sampling was resorted to with larger root systems.

The numbers of mycorrhizal tips per centimeter of root length found under the three environmental conditions were as follows:

3.6 in full light, A horizon present (17 seedlings)
2.6 in full light, A horizon absent (10 seedlings)
1.1 in partial light, A horizon present (29 seedlings)

Although all differences among these three values were highly significant, the extent of mycorrhizal development is not accurately reflected because the degree of proliferation of the infected tips cannot be shown.

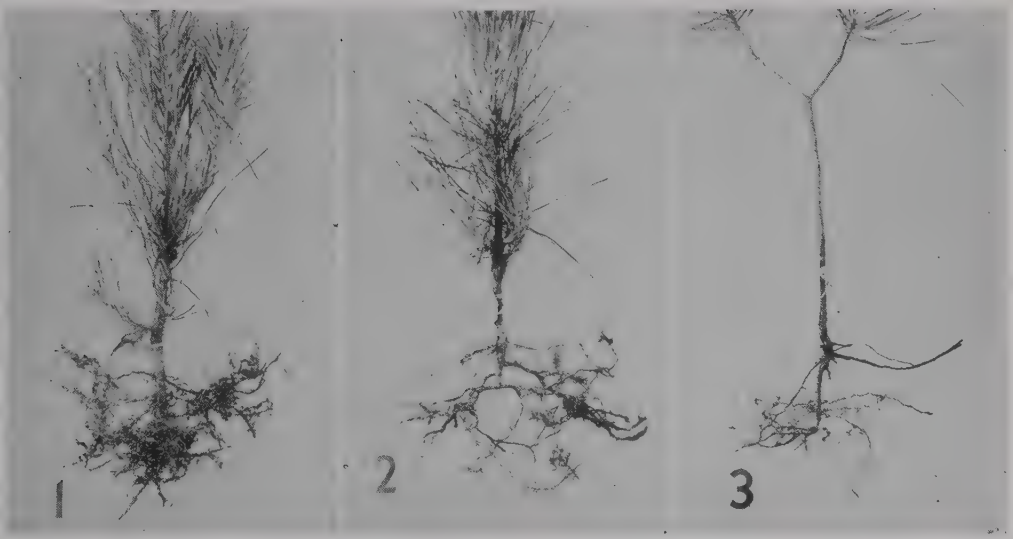


FIG. 1. Best mycorrhizal development with (A) A horizon present, (B) A horizon absent, and (C) within a pine stand.

Another group of seedlings was collected from the same locations the following June. However, instead of counting infected tips as before, three seedlings showing best, moderate, and poorest development of mycorrhiza were chosen from the sample of each location and photographed. The best development for each location is shown in Figure 1.

In addition, several blocks of soil were lifted within the pine stand at spots well away from any seedlings. The root fragments found in them therefore presumably were from the large overstory pines that were receiving ample light. Again, fragments showing best, moderate, and poor development of mycorrhiza were chosen and photographed. The best development of mycorrhiza is shown in Figure 2.

DISCUSSION

It is evident from the counts of infected roots and the pictures that there was a strong relation between the light intensity under which the seedlings were growing and the amount of mycorrhizal development. Since it has been amply demonstrated that carbohydrates are produced in accordance with the amount of light received by plants, Björkman's theory concerning the relation between surplus carbohydrates and mycorrhiza formation may be regarded as corroborated for the conditions of this study.

Of some interest also is the more extensive development of mycorrhiza that is associated with the presence of the A horizon. With the A horizon undisturbed, sources of infection might be more numerous so that root tips are more frequently attacked. A somewhat less likely reason is that mycorrhiza are able to utilize carbohydrates from the substrate as well as from the host plant (MacDougal and Dufrenoy 1944). The A horizon, containing a much greater quantity of carbohydrates than the B horizon, thus might support a greater development of mycorrhiza.

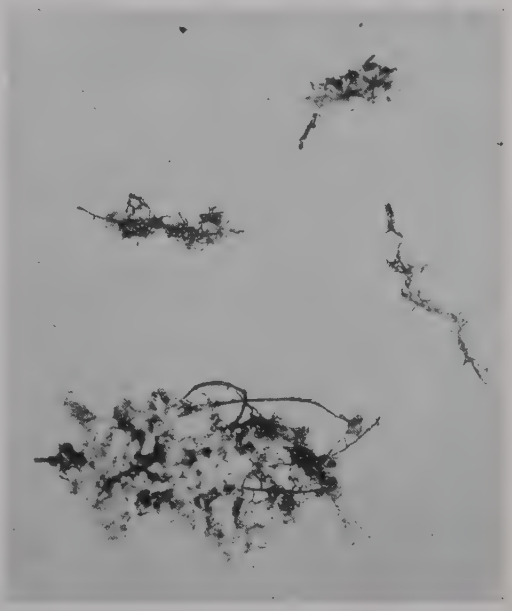


FIG. 2. Root fragments of overstory pine trees. Best mycorrhizal development. (Compare with Fig. 1.)

REFERENCES

Björkman, E. 1942. Über die Bedingungen der Mykorrhizabildung bei Kiefer und Fichte. (English summary: On the conditions for the formation of mycorrhizae in pine and spruce.) Symbolae Botanicae Upsalienses **6**, No. 2.

———. 1949. The ecological significance of the ectotrophic mycorrhizal association in forest trees. Svensk Bot. Tidskr. **43**: 224-262.

Hatch, A. B. 1935. The physical basis of microtrophy in pines. Black Rock Forest Bull. **6.**

MacDougal, D. T., and J. Dufrenoy. 1944. Mycorrhizal symbiosis in *Aplectrum, Corallarhiza,* and *Pinus.* Plant Physiol. **19**: 440-465.

Stålfelt, M. G. 1924. Untersuchungen zur Okologie der Kohlensaure—assimilation der Nadelbaume. Medd. Stat. Skogfors.—anst. **21**: 181-258.

KARL F. WENGER
TIDEWATER FOREST RESEARCH CENTER,
SOUTHEASTERN FOREST EXPERIMENT STATION,
U. S. FOREST SERVICE,
FRANKLIN, VIRGINIA

HEXAGENIA (EPHEMEROPTERA) POPULATION RECOVERY IN WESTERN LAKE ERIE FOLLOWING THE 1953 CATASTROPHE

Studies made in autumn 1953 (Britt 1955), following a period of stratification and low oxygen conditions, showed that the number of Hexagenia (Ephemeroptera) nymphs of the deeper water of western Lake Erie was greatly reduced. The nymphs appeared to be entirely eliminated from some areas where the water was deepest and where the bottom mud contained large quantities of organic matter. In channels and in shallow water around the shores and bays, a portion of the population survived.

Further studies have been made to determine whether the mayflies will repopulate the affected areas or will be succeeded by other bottom fauna. Methods and equipment were the same as those used in the 1953 study. Bottom fauna collections were taken from the same areas or stations as those of 1953. The locations where collections were made are shown in Figure 1.

On June 8, 1954, dredgings were made at four stations south and southwest of Rattlesnake Island. These collections yielded 70, 20, 35, and 45 very small nymphs per square meter. This was an average of 42.5 nymphs per square meter per station. This is approximately one tenth the normal population for this area (Britt 1955).

Since the autumn 1953 collections from these stations had yielded no live nymphs, a question arose as to where these small nymphs had come from and how they had managed to get into these areas. There are two possible answers to this question. (1) It is possible that the nymphs may have migrated from the shallow water where a part of the normal population had survived. During autumn, winter, and spring, strong currents are common in this area. Therefore, any nymphs swimming or moving over the surface of the mud could have been swept along and deposited at a new location. (2) All specimens collected at these stations in the spring of 1954 were extremely small, appearing to have passed through no more than four or five instars. This suggests the possibility that some of the eggs may have passed through the period of low oxygen concentration in a dormant state and hatched either very late in the autumn or early in the spring. Britt (paper in preparation) has demonstrated that in some species of mayflies there is a definite diapuase. Whether any of the eggs of Hexagenia go through a dormant state is unknown, but the following experiment indicates that some the eggs remain unhatched for long periods of time even at room temperature.

On June 28, 1954, eggs were removed from an adult *Hexagenia limbata.* These were placed into a petri dish half full of lake water. The dish was then placed on top of a table where air could circulate freely over the water surface. Temperature varied, but for the following three months it was well above normal room temperature. The eggs began to hatch on July 11. The greatest hatching rate occurred about July 20. A few eggs were still hatching by August 29. At this time the petri dish and the remaining eggs were transferred to a refrigerator where the temperature was just above freezing. On October 11 the eggs were moved to a constant temperature of 11°C. Examination on October 28 showed that a few eggs had hatched while at this temperature. The eggs were then placed at constant temperature of 22°C. Two days later, October 30, ninety new hatches had occurred. The remaining eggs were again put into the refrigerator near the freezing unit and unfortunately the water froze. On December 23 the frozen collection was brought back to room temperature. Observations over the period from December 23, 1954 to January 6, 1955 revealed no hatches.

This experiment showed that although the major portion of *Hexagenia limbata* eggs hatched within about a month at room temperature, some of the eggs hatched after a period of several months. Such a wide difference in hatching time indicates a phenomenal difference in metabolic rate. The causes of this difference are unknown at the present time. It appears, however, that the eggs having the lower metabolic rate could survive at a reduced oxygen concentration. The stratified conditions in western Lake Erie were broken up by wind action on September 4, 1953. According to the above experiment, there should have been a few unhatched eggs of Hexagenia remaining on the bottom at this time. Since the water temperature was above 11°C. until November 5, 1953 and after April 26, 1954 until the four collections were made, there was ample time for such hatches to occur. The sizes of the specimens found in the June 8 collections appear to substantiate this theory.

The autumn 1954 collections were made at the same stations as those of 1953. The results from these collections are shown in Figure 1. In order to make comparison of results easy, the results of the 1953 collections are also included.

Although 10 stations had slightly lower numbers of nymphs in 1954 than in 1953, the overall average was much greater in 1954. The average for the 61 stations in 1954 was 827.5 nymphs per square meter as contrasted with the average of 44.3 nymphs per square meter at the same stations in 1953. This was about 18.7 times the autumn 1953 population.

The 23 stations within the acute angle drawn on Figure 1 had an average of 235 nymphs per square meter in 1954 contrasted with 112 in 1953. This was about 2.1 times the 1953 population. The spectacular increase in populations was that of the stations lying outside this acute angle. The 38 stations in this area had an average of 1186.2 nymphs per square meter in 1954, but they had

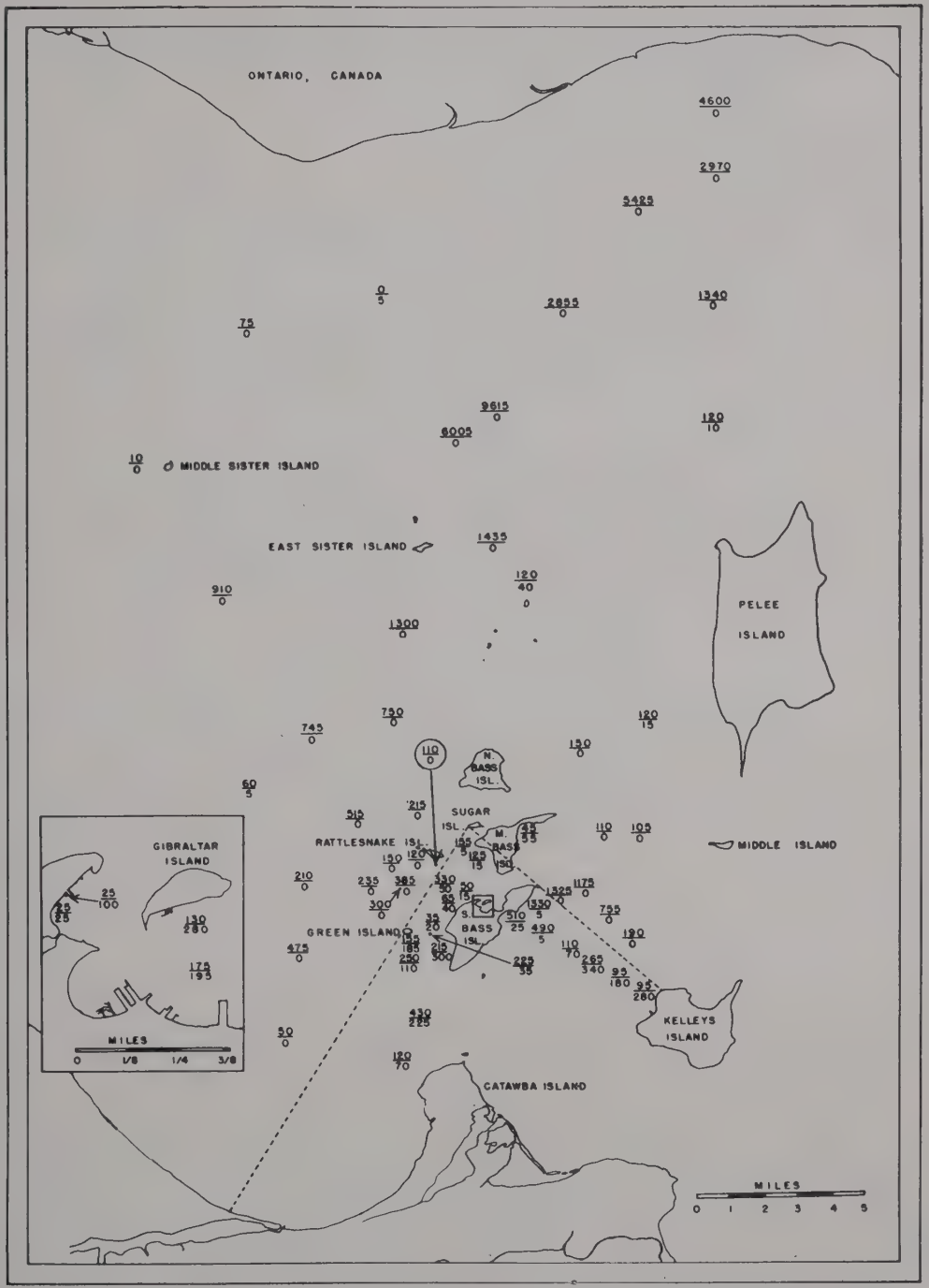


FIG. 1. Map showing the part of western Lake Erie where the collections of Hexagenia nymphs were made. In each group of numbers, the top group represents the number of Hexagenia nymphs per square meter in that area in autumn 1954; the bottom number represents the number of nymphs found at the same place in autumn 1953. EXAMPLE: $\frac{120}{40} = 120$ nymphs/sq. m. in 1954 and 40 nymphs/sq. m. in 1953. The station within the circle should be located south of Rattlesnake Island near the point of the arrow.

an average of only 3.4 nymphs per square meter in autumn 1953. This indicates that in this area the 1954 population was about 349 times that of 1953.

Discussion

From the foregoing results, it appears that the 1954 population of Hexagenia compares favorably with those of other years. Wright and Tidd (1933: 279), using data from only a few stations, estimated the average populations of Hexagenia in western Lake Erie as 283 and 510 nymphs per square meter in 1929 and 1930, respectively. Calculations (Britt 1955) from data collected by Wood (Wood 1953) from 150 stations in this study area in 1952 and 1953 gave an estimated average of about 320 nymphs per square meter. In a more restricted area south of Rattlesnake Island (indicated by circle and arrow in Fig. 1), Chandler (personal communication) found averages of 493 and 351 nymphs per square meter in 1942 and 1943, respectively. In this same area I collected 388 and 300 nymphs per square meter in June of 1952 and June of 1953, respectively.

Although the distribution of Hexagenia in 1954 appeared to be uneven, the average number of nymphs per square meter appeared to be equal to or slightly above normal. This rather high average may be due to the fact that almost all the population was composed of the small first-year nymphs whose numbers had not yet been reduced by such environmental factors as predators, low temperatures, currents, etc.

One of the interesting problems arising from this study is why the stations in the channels and near the shores (within the acute angle of Fig. 1) did not show a greater increase in numbers of nymphs in 1954. About one third of these stations had even smaller numbers than in 1953. Some of the factors which may have been responsible for this are: (1) Wind direction and velocity at the time of mating flight may have caused most of the eggs to be deposited elsewhere. (2) Water currents may have been sufficiently strong to prevent the settling of eggs in the area or to have swept away recently hatched nymphs. (3) Intraspecific competition by the relatively large population already inhabiting the area may have been so great that only a few of the recently hatched individuals were able to survive. (4) Type of bottom may have influenced the size of the population. Within the acute angle on Figure 1 a large portion of the bottom is hard, with soft mud occurring only in limited areas. However, all the stations were located on mud bottom.

It is impossible at the present time to determine which of these factors, if any, was responsible for holding down the average number of nymphs in this area while the average number of nymphs outside this area was five times as great. Perhaps no one factor but rather a combination of factors may have been responsible for this difference.

Summary

1. Bottom fauna collections made in June, 1954, from areas in western Lake Erie where the Hexagenia population had been entirely eliminated by low oxygen conditions in autumn 1953, revealed that a few nymphs were again inhabiting the area.

2. It was concluded that the nymphs either migrated from shallow water or hatched from dormant eggs which had remained in the area during the short period of stratification in autumn of 1953.

3. It was shown experimentally that although most Hexagenia eggs hatched within 3 to 5 weeks at room temperature, some of the eggs did not hatch until several months later.

4. The average number of nymphs for the 61 stations in autumn 1954 was about 18.7 times the average for the same stations in autumn 1953.

5. All areas did not show the same increase in populations. In channels and near shore the average 1954 population was only 2.1 times that of autumn 1953, but in the deeper, more extensive areas, the average 1954 population was about 349 times that of 1953.

References

Britt, N. Wilson. 1955. Stratification in western Lake Erie in summer 1953: Effects on the *Hexagenia* (Ephemeroptera) population. Ecology, **36**: 239-244

Wood, K. G. 1953. Distribution and ecology of certain bottom-living invertebrates of the western basin of Lake Erie. Unpublished dissertation, The Ohio State University.

Wright, S., and W. M. Tidd. 1933. Summary of limnological investigations in western Lake Erie in 1929 and 1930. Trans. Amer. Fish. Soc., **63**: 271-285.

N. Wilson Britt

Ohio State University,
Institute of Hydrobiology,
Put-in-Bay, Ohio

INSECT ATTACKS ON NATIVE AND PLANTATION PINES IN CENTRAL WISCONSIN

In the spring of 1948, a tree plantation was started in Adams County on the sand plains in the bed of Glacial Lake Wisconsin. The predominant native forest species in this region are jack pine (*Pinus banksiana* Lamb.) and northern pin oak (*Quercus ellipsoidalis* E. J. Hill). Smaller numbers of red pine (*P. resinosa* Ait.), white pine (*P. strobus* L.), red oak (*Q. rubra* L.), white oak (*Q. alba* L.), and trembling aspen (*Populus tremuloides* Michx.) are also found.

The plantation site (SW ¼ SW ¼ Section 23, T17N R6E) is a level fifteen acre field which was abandoned about 25 years ago. The soil is a well-drained Plainfield sand with a water table about 5 feet below the surface.

In 1941, 7 years previous to the acquisition of the land by the authors, about 500 jack pines were planted. In the spring of 1948, 7,000 jack pines plus 10,000 trees of other species were planted. Spacing was approximately 6 ft. by 6 ft. Extending into the plantation is a belt of native jack pine reproduction ranging in age from 5 to 15 years. A few older seed trees are scattered here and there. (See Fig. 1.)

When the authors visited the plantation in November, 1952, it was immediately apparent that the plantation jack pines were much more heavily attacked by insects than was the natural reproduction. Consequently, a count

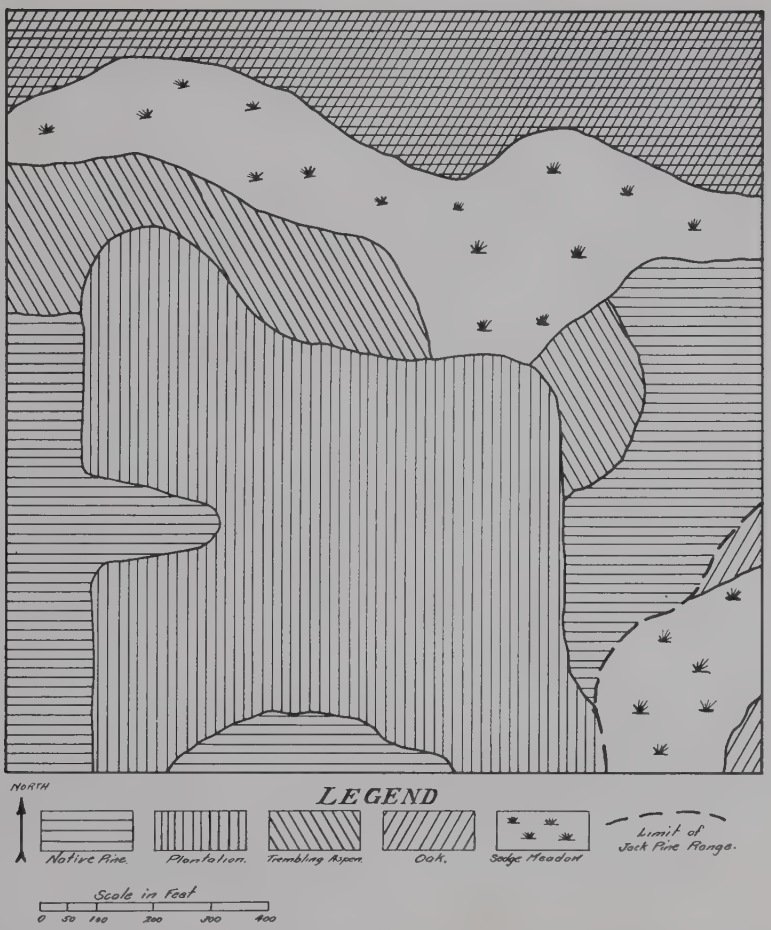


FIG. 1. Map of 40 acre tract, including pine plantation.

of all the jack pines was made, and comparative figures were obtained.

It was found that the root collar weevil (*Hylobius radicis*) had damaged 59 per cent of the 1941 plantation stock but had attacked only 7 per cent of the native trees. No injury to smaller stock, native or plantation, was observed. The weevils did not seem to have entered trees less than 2 inches in diameter at ground level.

The smaller jack pines were, however, infested with pitch twig moths (*Petrova* sp.). Almost every planted tree was injured, but very few of the others were attacked. The count showed that 61 per cent of the terminal shoots on plantation trees were dead or deformed, while on native reproduction of similar size, only 3 per cent had been invaded. In addition to the infestation by the pitch twig moth, a few trees were found to have been attacked by the white pine weevil (*Pissodes strobi*) and by the pine spittle bug (*Aphrophora parallela*), but damage by these insects was negligible.

When these data were taken, it was thought that this study would continue over a period of years before any results were presented. However, in April, 1953, a forest fire burned over 1,556 acres, including this plantation.

Several factors may be involved in the attack of insects on these jack pines:

1. In the accompanying figure, a part of the apparent southeastern limit of the continuous range of jack pine in Wisconsin is shown. Seed for the nursery stock came from northern Wisconsin, well within the range, and consequently may not have been adapted to this locality.

2. The native pines grew closer together than did the plantation pines and were closer to larger trees. It is possible that more widely spaced trees are more subject to infestation than are those growing close together. It is also likely that the older, taller trees sheltered the reproduction close to them from attack.

3. When seedlings are transplanted, a certain amount of damage is done to them. This may weaken them just enough initially to make them easy prey of insects.

ROBERT T. BROWN
EUGENE P. YOUNG

DEPARTMENT OF FORESTRY,
MICHIGAN COLLEGE OF MINING AND TECHNOLOGY,
HOUGHTON, MICHIGAN
AND
INFILCO, INC.,
TUCSON, ARIZONA

NEW METHODS OF COLLECTING BOTTOM FAUNA FROM SHOALS OR RUBBLE BOTTOMS OF LAKES AND STREAMS

Most limnologists and fisheries biologists are aware of the difficulties encountered in collecting bottom fauna from lake shoals and stream riffles. Several types of dredges give good results on soft bottom soils, but none of these give satisfactory results on shoals and riffles where the bottom is composed of rubble and coarse gravel. Other devices such as the Wilding square foot sampler and the Surber square foot stream sampler have been used with varying degrees of success. One method generally used by limnologists and fisheries biologists for a quick survey of shoal or riffle fauna is to remove stones from the bottom and pick or wash off the animals found on the stones. By this method only the animals which cling to the stones are collected. Two other sources of error are: (1) Many of the forms are able to conceal themselves and thus escape detection; this is especially true of the very small individuals. (2) Some forms exhibit strong positive thigmotactic and negative phototactic responses. Thus they are difficult to wash from the dark lower sides of the rough-surfaced stones.

Wodsedalek (1911) showed that the normal negative phototactic response of the nymph of the mayfly, *Stenonema interpunctata* (Say), could be reversed by submerging the nymph in a 0.03 to 0.09 per cent solution of strong acids or bases or in an 0.8 per cent solution of alcohol. Similar results were reported by Loeb in 1904 (Wodsedalek 1911: 269) for *Gammarus pulex* and by Jackson in 1910 (Wodsedalek 1911: 269) for *Hyalella azteca*.

This knowledge of the effects of chemicals on these animals appeared to offer a practical application in collecting these and similar forms from shoals. If a small amount of chemicals would cause a positive phototactic response in these animals, would this not cause them to leave the dark stones and move toward light? Some trial collections were made to test this theory. The results were so good that since then I have used this method as standard procedure in collecting the clinging forms of mayfly nymphs. My methods are given below:

Quick Survey Method

Six quarts of a 2-5 per cent solution of alcohol were placed in a ten-quart white enameled pail. To this enough HCl was added to make a concentration of about 0.03 to 0.06 per cent. Stones were removed from the bottom and agitated for a few seconds in this solution. When a stone touched the solution, many organisms, especially the sprawling and clinging forms of mayfly nymphs, were observed to leave their dark hiding places on the stone and to begin swimming around in the solution. After treating several stones, the chemical mixture was poured through a set of U. S. Standard sieves to remove the animals and accumulated debris. The collected material was then washed gently but thoroughly in clean lake water. After this wash, the animals, especially mayfly nymphs, appeared to regain their normal negative response to light and showed no indication of ill effects from the chemical bath. This material was then put into white enameled pans containing about one half inch of lake water. The mayfly nymphs were easily separated from the debris and most other forms of animals by floating a few dark-colored wooden chips on the surface of the water. The mayfly nymphs now showing a negative response to light and a positive thigmotactic response attached themselves to the dark lower surfaces of the chips.

When the chips had a large number of nymphs attached, they were transferred to other containers. If the nymphs were to be kept alive for study, the chips were put into containers filled with lake water. For preserved specimens, the chips with nymphs attached were dropped into petri dishes filled with 70-95 per cent alcohol or with a killing solution such as KAAD (Peterson 1948: 6-8). The few nymphs which failed to attach and all other

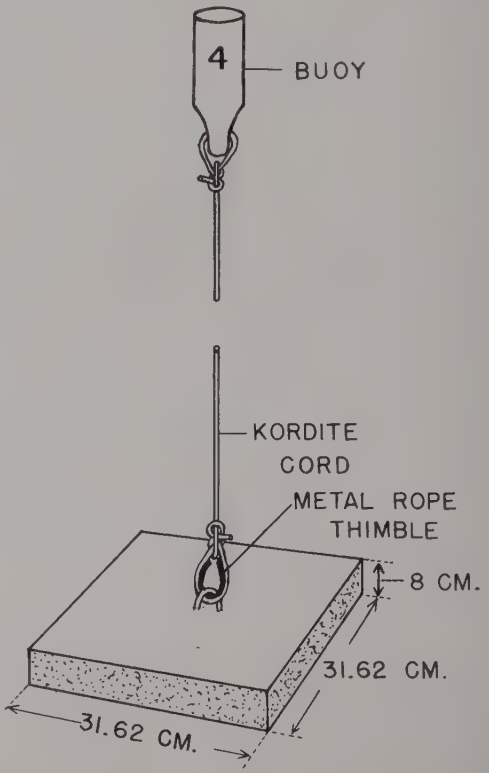


FIG. 1. Diagram showing concrete block with buoy attached. Bottom view shows where the bottom surface was scored before the concrete had hardened.

animals were removed from the pan by use of forceps and medicine dropper.

This method of collecting is fast and gives very clean collections. Since it is necessary to use forceps for only a part of the collection, there is a minimum of damaged specimens. Probably the most important advantage of this method is that it is effective for even the smallest specimens which could not be collected satisfactorily by other methods.

Collections from Deeper Water

Stones are quite difficult to locate and bring to the surface when the water is more than about a meter in depth. In order to overcome this difficulty, concrete blocks 31.62 cm. square (1/10 sq. m.) and about 8 cm. thick were constructed with a ring for attaching a cord and buoy (Fig. 1). Blocks for use in ponds or other quiet waters could be made thinner, but for use in rough water they must be relatively heavy to prevent movement by wave action. When the blocks were made, the bottom surface of each was scored with a sharp tool before the concrete had hardened. This gave a network of shallow scratches or grooves in which small organisms could conceal themselves. Since the blocks were similar to the stones in the normal habitat, animals migrated from the stones to the blocks where they were able to conceal themselves and to feed on the detritus and the algal growth that soon covered the blocks.

I have observed that the position of a stone on the bottom, that is, whether the stone is pressed into the bottom or is held up by other stones so that water currents pass under it, greatly influences the size of the animal population inhabiting the stone. Since it was impossible to place the blocks in uniform positions relative to the bottom, the best way to overcome this difficulty appeared to be to use several blocks at each station to obtain an average population. Therefore four blocks were placed on the bottom at each station. A larger number of blocks at each station probably would have given a little more reliable sample of the average population, but this would have increased the task of making the collections. The stations were located on gravel and rubble bottom in water ranging from one half to five meters in depth. The blocks were usually left on the bottom from one to four weeks.

Kordite, a cord consisting of strong fibers and three small flexible wires enclosed in a plastic sheath, was found to be superior to rope for attaching the buoys since it did not deteriorate over long periods of time. Being small in diameter, it offered minimum resistance to water motion thereby lessening the chances of movement of the blocks by strong currents and wave action. However, the small diameter of this material had one serious drawback; it was difficult to grasp securely when lifting the heavy concrete blocks.

When the blocks were lifted they were dipped into a tub containing the same mixture of water, HCl, and alcohol as that used on stones when collecting in shallow water. Methods of separating the organisms from the debris were the same as those used for the shallow water collections.

Collections made in this manner yielded as high as 7,570 organism per square meter of bottom. In some instances the mayfly nymphs alone numbered more than 1,300 per square meter.

References

Peterson, Alvah. 1948. Larvae of insects, an introduction to Nearctic species, Part 1. Lepidoptera and plant infesting Hymenoptera. Ann Arbor, 315 pp.

Wodsedalek, J. E. 1911. Phototactic reactions and their reversal in the mayfly nymphs *Heptagenia interpunctata* (Say). Biol. Bull., 21: 265-271.

N. Wilson Britt

Ohio State University,
Franz Theodore Stone Institute of Hydrobiology,
Put-in-Bay, Ohio

A SIMPLE METHOD OF ESTIMATING LOW LIGHT INTENSITIES

It is never easy to find the correct way to measure light intensities in connection with ethological problems. For studies on crepuscular and nocturnal animals this factor is of special importance and at the same time the difficulties of measurement are still greater than in the daytime.

During our current study of flight habits in mosquitoes, it became necessary at one time for us to improvise, on short notice, a method for obtaining at least a rough estimate of the light intensity during a considerable part of the night. Exposure meters, such as are used in photography, are usually not able to measure the illumination later than 10-15 minutes after sunset, or about half of the duration of civil twilight which in Florida lasts 23-26 minutes. The following inexpensive and easily provided method of estimating low light intensities may, as a temporary expedient, be useful for other biologists in a similar situation.

The principle is a very old one, indeed. Moslems, during the month of Ramadan, fast during the daytime; and the beginning of the day is determined according to the Quran: "Eat and drink until the white and black threads at dawn become distinguishable to you." Still older is the direction in the Talmud that the Shewa Prayer shall begin when it is possible to distinguish between purple and white.

Since we needed indications of more than one light intensity, we used a number of 2-color combinations. We tried many combinations on different backgrounds and found the ones tabulated below to be the most useful. We used no. 50 cotton threads of the following colors: (mfr: J. & P. Coats Co.) black, white, dark green, blue-4B, red, orange-36C, and (mfr: American Thread Co.) yellow 529.5. Two pieces of thread, about 30 cm. long, were cut of two different colors and twisted together to form an irregular ball a couple of centimeters in diameter. The several balls were then glued to a white-painted board. In use the board was placed where the illumination was to be measured and the moment of merging recorded, *i.e.* the moment when the two colors in a ball can no longer be distinguished. In order to eliminate individual differences in visual sensitivity the same person should always make the observations. The manner of taking the observations should be standardized as much as possible. The observer must make sure his

eyes are fully adapted and he should avoid looking at any bright light during the period of observation.

To calibrate this device, the observer stationed himself with the board in the usual position in a dark room with a door open to a room lighted by daylight. Variations in illumination were established by changing the opening of the door. A photocell was placed as close as possible to the thread-ball merging at the illumination in question. In preliminary tests a barrier-layer photocell connected to a Lange galvanometer was used; in the final test we used the "search unit" of a Photovolt electronic photometer, model 514-M.

In some of the early tests incandescent lights were used in calibration and the results did not differ significantly from calibrations by daylight. The error introduced in calibrating by midday light a device for measuring crepuscular light (with its preponderance of long-wave light) is therefore presumed to be negligible.

The results from two series of measurements made on different days, one in the morning and the other in the afternoon, are given in Table I. A series of actual observations is given in Table II. These data will indicate the range of adaptability for the method.

TABLE I. *Illuminations determined for the merging points of colored thread combinations.*

Thread combination	*Lux at moment of merging.*	
	Exp. 1	*Exp. 2*
Green-blue	2.15	2.30
Green-black	1.51	1.35
Red-blue	0.64	0.41
Orange-green	0.32	0.30
Red-yellow	0.19	0.22
Blue-white or red-white	0.06	0.09
Green-white	0.02	0.06
Black-white	0.01	0.03

TABLE II. *Merging moments for colored thread combinations and corresponding light measurements on a moonless evening. Sunset at 18h41′; civil twilight ending at 19h05′.*

Thread combination	*Time of merging*	*Lux*
Green-black	19h00′	1.4
Orange-green	19h20′	0.3
Red-yellow	19h26′	0.2
Red-white	19h35′	0.08
Blue-white	19h40′	0.08
Green-white	19h41′	0.04
Black-white	19h46′	0.02

For authenticating the origins of this millenium-old method we should like to express our sincere gratitude to Prof. Dr. Pedersen, Copenhagen, and Dr. Mahomed Bey Hussein, Dokki, Egypt.

REFERENCES

El Quran. Sura 2 vers 184.
Talmud. Mishna Berchoth. I, 2.

ERIK TETENS NIELSEN
JAMES S. HAEGER

BUREAU OF ENTOMOLOGY
FLORIDA STATE BOARD OF HEALTH
VERO BEACH, FLORIDA

DIFFERENTIAL MORTALITY FROM HIGH TEMPERATURE IN A MIXED POPULATION OF FISHES IN SOUTHERN MICHIGAN

Mass mortality of fishes in nature is not especially rare, but most often the phenomenon develops so unexpectedly that no biologist is on hand to trace its course or to identify the cause, except by inference. Often multiple causative factors are involved, and no simple explanation is possible. Death from heat stroke appears to be most unusual, but has been noted for salmonid and other fishes in streams in the Canadian Maritime Provinces by Huntsman (1942 and 1946). The occasion of a recent visit to a Michigan lake on a hot summer afternoon coincided, fortuitously, with the peak of a mass mortality of fishes. A favorable opportunity was provided to determine not only that high temperature was responsible, but to obtain a rather good assessment of the differential tolerance to high temperature among the several species of fishes present and between small and large fish within species.

The site of the catastrophe was a shallow bay on the east side of Bass Lake, on the property of the Pleasant Lakes Club, T. 1 N., R. 5 E., Sect. 28, about one mile southwest of Lakeland, Livingston County, Michigan. The bay was essentially undisturbed except that a gravel causeway, which had been placed across the neck of the bay after the ice breakup in the spring of 1952, deprived the fish from access to the lake proper. On June 5, 1952, the resultant pond was some two acres in extent and had a maximum depth of about 18 inches. On this date 25 adult females of a northern-hardy stock (Krumholz 1944) of *Gambusia affinis affinis* were placed in the pond. By July 12, the day of the observed mortality, drought had so reduced the water level that the surface area was not more than one-fourth acre and the maximum depth was five inches. The bottom of the pond, like that of the entire littoral zone of the lake, is composed of marl. (Raymond, 1937, has studied the limnology of Bass Lake.) The macroscopic vegetation was scanty, consisting of Chara, and there was no shade or protecting cover. For the preceding two weeks the pond had been under casual daily observation. An abundance of small fish was noted, but there was no indication of unusual mortality either as evidenced from the presence of dead fish or from observed predation. This period was unusually warm, as shown by records of the meteorological station at the University of Michigan's Edwin S. George Reserve, located about eight miles west of Bass Lake (Fig. 1). It is assumed, therefore, that the fish present in the pond were thoroughly acclimated to a high temperature. The observed mortality, then, was due to temperature in excess of the lethal limit rather than to rate of temperature change which may be fatal within the range of toleration if the fish are not fully acclimated (Brett 1946, and included references).

MASS MORTALITY

July 12 was a bright hot day: in midafternoon the shade temperature at the pond was 33°C (91.4°F) and the water was 38°C (100.4°F). The latter figure was uniformly maintained as verified at several points in the

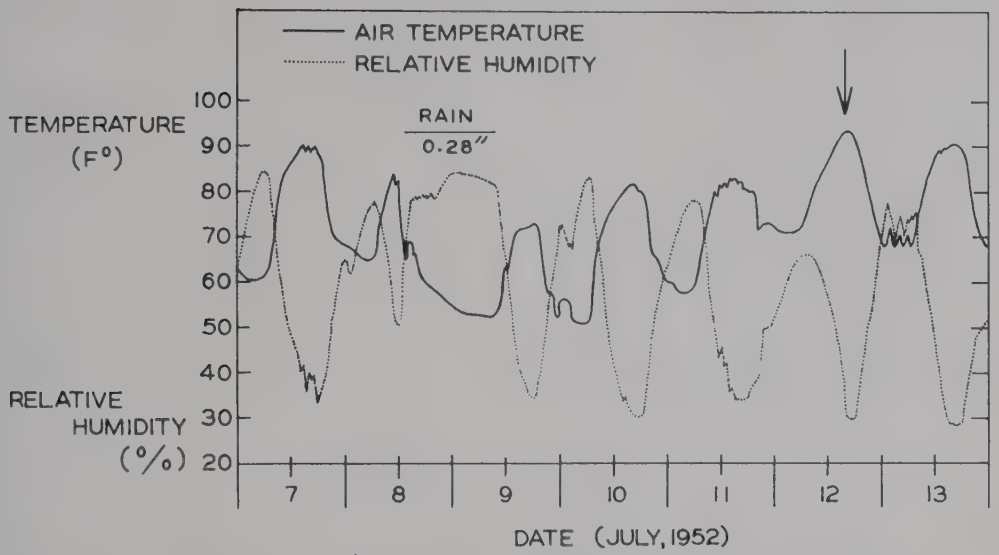


FIG. 1. Meteorological record at the Edwin S. George Reserve, 8 miles west of Bass Lake, for the period before and immediately after the time of fish mortality due to heat stroke (indicated by arrow).

pond, and extended down at least an inch or two into the marl bottom. All fish in the pond were exposed to this temperature for a period of at least two hours and at nearly as high a level for several additional hours. Despite the high temperature a brisk breeze blew from the main lake all afternoon; waves several inches high were present on the lake and the surface of the pond was rippled. Although no determinations of dissolved gases were taken, a combination of physical factors in the pond (extensive water surface, shallow depth, moderate breeze, and predominantly inorganic bottom) make it obvious that there was a high oxygen content and a low tension of decomposition gases.

The mass mortality was first noticed at about 3:30 p.m., when fish of many species were dead or dying. All dead fish had succumbed recently, however, since their flesh was still firm. At the prevailing temperature decomposition would be so rapid as to be strikingly obvious within a few hours. The dying fish were sluggish and lethargic and most were lying on their sides and made little effort to escape capture; they could be approached rapidly and picked up by hand. There was no gulping of air at the surface as is typical of fish suffering from anoxia. The interpretation that distress and death were caused by high temperature rather than anoxia is confirmed not only by the behavior of affected fish but by the observation that dead fish did not have distended gills and gaping mouths, which normally attend suffocation. The absence of fish long dead and the serious distress of additional scores of individuals made it obvious that the mortality was a phenomenon of the moment. At high temperatures, loss of equilibrium and cessation of swimming and of breathing were reported to occur close together by Huntsman (1942), a series of events that was obvious also in these pond fishes. Death of nerve cells was held accountable, and once the sequence is initiated there is no recovery on lowering the temperature.

Not all fish were notably affected. The banded killifish (*Fundulus diaphanus menona*), the most abundant species present, was active and the adults fled precipitately when the observer approached. Only the young of this species could be caught in the hands and this seemed not to be caused by the high temperature. Although thousands were present, only two dead adults were seen; the others, including many young, seemed to be active and healthy. No specimens of *Fundulus notatus* were dead or in distress, and no individuals of *Gambusia* showed any sign of inconvenience. One sluggish bluegill (*Lepomis macrochirus*) and one affected pumpkinseed (*Lepomis gibbosus*), an adult 73 mm. in standard length, were picked up by hand, but many other sunfish observed were active and apparently not seriously disturbed by the high temperature. What was probably the only largemouth bass (*Micropterus salmoides*) in the pond, a yearling, was visibly sluggish but still sufficiently active to avoid capture. A single rock bass (*Ambloplites rupestris*) was in distress and two others were already dead (length range 50 to 58 mm.). With these exceptions the centrarchids were still active and subsequent study showed that all species except the rock bass survived.

In contrast to the hardiness displayed by the cyprinodontids, poeciliid, and centrarchids, death or affliction was the lot of the umbrid, a catostomid, the cyprinids, the ictalurids, and the single percid present. The mudminnow (*Umbra limi*) is commonly regarded as one of our hardiest fishes, as indeed it is if judged by tolerance to foul conditions, but it displayed a lower heat threshold than the bluegill. The several mud-minnows noted were already dead or in severe distress; none is known to have survived. Three juvenile (71 to 74 mm. long) chubsuckers, *Erimyzon sucetta,* were still alive but apparently dying; others seen were dead except that one young was swimming fairly well. Similarly, among the cyprinids, three half-grown and adults (55 to 68 mm. long) of the golden shiner, *Notemigonus crysoleucas,* were moribund, and others were already dead; four adults (44 to 47 mm.) of *Notropis heterodon* and eight (44 to 51 mm.) of *Notropis heterolepis* were dead or dying. Two

adults of *Notropis deliciosus* and one (45 mm.) of *Pimephales notatus* had died recently. It developed that catfishes have a lower temperature tolerance than one might have suspected. Single half-grown individuals of *Ictalurus nebulosus* (100 mm.) and *Ictalurus natalis,* and an adult (47 mm.) of *Noturus miurus* were all dying. The tadpole madtom (*Noturus gyrinus*) was abundant; scores of individuals were dead, an equal number were moribund, and a few young were still fairly active but could be caught easily in the hands. One hundred and sixty large juvenile and adults (36 to 68 mm.) and three young (15 to 16 mm.) were preserved, but many more were seen. Several adult (40 to 44 mm.) Iowa darters, *Etheostoma exile,* were found dead.

Recovery and Survival

Fish observed on July 13, when the pond was revisited, were either in an advanced state of decomposition, having died the day before, or were alive and displayed normal activity. Again the weather was hot but the water temperature was down to 35°C (95° F) and the air was 32°C (89.6°F). A second mercury-bulb thermometer was available and was used to verify the accuracy of the instrument used the preceding day. I could catch no fish in my hands. All survivors were obviously well within their limits of thermal tolerance.

On July 19 the pond was seined to determine what fish had survived the mortality of the previous week. Most of the remaining fish were caught and examined. By this time scavengers had apparently removed all dead fish. As was expected on the basis of earlier observations, thousands of young and hundreds of adults of *Fundulus diaphanus* were caught. Of 84 specimens preserved, 15 were young varying from 15 to 24 mm. in standard length and 69 were larger juveniles and adults from 35 to 63 mm. long. There were 10 adults of *Fundulus notatus* (37 to 56 mm.) and several young and adult gambusias. The surviving centrarchids included a yearling of *Micropterus salmoides* (96 mm. long), 1 young (15 mm.) and 5 adults (57 to 64 mm.) of *Lepomis cyanellus,* 4 juveniles (45 to 53 mm.) of *Lepomis macrochirus,* a juvenile and an adult (44 and 45 mm.) of *Lepomis megalotis peltastes,* and 4 young (17 to 18 mm.) and 22 half-grown to adults (47 to 80 mm.) of *Lepomis gibbosus.* No examples of *Ambloplites rupestris* appear to have lived.

Survival among the less tolerant species was restricted to a small number of immature fish. It seems highly probable on the basis of this evidence that for these species, at least, the young have a greater heat tolerance than do the adults. The survivors were: two young (22 and 23 mm.) of *Erimyzon sucetta,* one young (13 mm.) of *Notropis heterodon,* two young (17 and 23 mm.) of *Pimephales notatus,* one half-grown (95 mm.) of *Ictalurus nebulosus,* and one young (16 mm.) of *Noturus gyrinus.* This observation is in accord with the findings of Huntsman (1942) for Atlantic salmon and of Hart (1952: 54) for two species of cyprinids, that large fish died before smaller ones. In *Lepomis macrochirus,* however, Hart found that smaller fish died before the larger.

Discussion

The temperature in the pond at the time of the mortality (38°C) should not be interpreted as necessarily being below the maximum lethal threshold for those species that survived, at least for purposes of comparison with Brett's (1946) determinations. Brett defined the upper lethal temperature, for a given acclimation level, as that temperature at which fifty per cent of the fish die if exposed for a period of twelve hours. Since the mortality here reported resulted from much shorter exposure to maximum temperature, the true upper lethal is probably somewhat lower than might be inferred from these data alone.

Hart (1952) believed that lethal temperatures of the species investigated by him are well above the thermal extremes usually encountered in their natural environments, and that these physiological characteristics have little ecological significance. The mortality here reported is one of the infrequent exceptions to this generalization, but it resulted in part from human intervention—the construction of the gravel causeway that restricted free egress from the area.

In the natural fish mortalities studied by him, Huntsman (1942 and 1946) found that prior to mortality a high moisture content in the air contributed to high water temperature by reducing radiant heat loss. The relative humidity was falling at the George Reserve, eight miles away, during the two days preceding the mortality at Bass Lake (Fig. 1), so no such effect is evident in this observation. However, in the absence of a record of local humidity conditions at Bass Lake preceding the mortality, it is conceivable that a low-lying fog was present over the pond on the night of July 11-12, and that the blanketing effect contributed to the high water temperature that developed on July 12.

Acknowledgments

Dr. J. Sanford Hart and Dr. Charles F. Walker have graciously read the manuscript and offered suggestions. Dr. Irving J. Cantrall kindly furnished meteorological records. My son, David R. Bailey, assisted in the field observations.

Summary

A temperature of 38°C resulted in high mortality to the fishes confined in a shallow pond. Symptomatic of distress was a marked lassitude, loss of orientation, and reduction of swimming ability. At a subsequent temperature of 35°C survivors had normal powers of locomotion and activity. For those species of which some fish lived and others died, only immature fish survived. The mortality was differential as regards species, the umbrid, catostomid, cyprinid, ictalurid, and percid species mostly being killed, whereas the cyprinodontid, poeciliid, and centrarchid species (except *Ambloplites rupestris*) survived.

References

Brett, J. R. 1946. Rate of gain of heat-tolerance in goldfish (*Carassius auratus*). Univ. Toronto Stud., Biol. Ser., no. 53; Publ. Ont. Fish. Res. Lab., **64**: 1-28, figs. 1-8.

Hart, J. S. 1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. Univ. Toronto Stud., Biol. Ser., no. 60; Publ. Ont. Fish. Res. Lab., **72**: 1-79, figs. 1-18.

Huntsman, A. G. 1942. Death of salmon and trout with high temperature. Jour. Fish. Res. Bd. Canada, **5**: 485-501, figs. 1-3.

———. 1946. Heat stroke in Canadian Maritime stream fishes. Ibid., **6**: 476-482.

Krumholz, Louis A. 1944. Northward acclimatization of the western mosquitofish, *Gambusia affinis affinis.* Copeia, **2**: 82-85.

Raymond, M. R. 1937. A limnological study of the plankton of a concretion-forming lake. Trans. Amer. Micro. Soc., **56**: 405-430, fig. 1.

Reeve M. Bailey

Museum of Zoology,
University of Michigan,
Ann Arbor, Michigan

OBSERVATIONS ON ANCHOR ICE IN A MICHIGAN TROUT STREAM[1]

Anchor ice is a spongy flocculent mass of ice crystals which forms on stream beds in certain northern areas. Several workers have suggested possible biological influences of anchor ice (Hubbs and Trautman 1938; Needham 1938; Hazzard 1941). Maciolek and Needham (1952) described the conditions for occurrence and influences of anchor ice in Convict Creek, California, and Brown *et al.* (1953) conducted a similar study on the West Gallatin River, Montana.

During the winter of 1951-52, observations were made on anchor ice in the Pigeon River, Otsego County, Michigan. The purpose was to determine the possible influences of this ice on stream ecology. The Pigeon River has hard water (methyl orange alkalinity 126-206 ppm), an average winter flow of about 40 cubic feet per second, and is populated with brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), rainbow trout (*Salmo gairdneri*), and several smaller species.

Heat loss from the stream bottom by radiation during the night is believed to be responsible for anchor ice formation (Barnes 1928). In sub-freezing clear weather, the stream bed may lose enough heat to reach a temperature of a few thousandths of a degree below 0°C. Water at the bottom of the stream then forms ice crystals. It is believed that anchor ice forms when these crystals become attached to the supercooled stream bed. Anchor ice will not form when surface ice is present since surface ice prevents the loss of heat by radiation.

Observations

In the Pigeon River, anchor ice formed during clear nights (barometer rising) when the air temperature fell below minus 15.6°C. and was observed on five days from November 26, 1951 to March 7, 1952. This ice formed most commonly in sections of the stream bed possessing the fastest-flowing and most turbulent water and appeared to a lesser extent in slower moving water. It was never observed in quiet eddies. The depth of the stream where anchor ice formed varied from 6 to 24 inches. The ice formed on stones and debris of the stream bottom and, therefore, had a rough, wavy appearance. The mean thickness of anchor ice was about two inches although it reached a maximum of seven inches. Maximum thicknesses were always observed in the fastest-flowing water. Apparently solar radiation in the daytime causes the ice to rise to the surface and it then floats downstream. Usually all ice had been released by 10 A.M. Anchor ice persisted for one 48-hour period because of heavy overcast and reached its maximum thickness.

A recording stream-flow gauge showed that water flow decreased gradually during the formation of the ice. Anchor ice thus formed temporary retaining dams on the stream bed. When the ice was loosened, a large amount of stored water was released which caused an abrupt increase in volume of flow. This minor flooding had no observable scarring effect on the stream bed.

A Surber bottom sampler was used to collect samples of ice on the stream bottom (Surber 1938). The brass frame of the sampler was adequate to cut the ice. Prior to its release by natural causes, the ice could be easily released manually by carefully lifting it off the gravelly bottom and allowing it to flow into the sampler net. The ice was then taken to the laboratory where it was melted; all the materials and organisms therein were analyzed. Ten samples of one square foot each were collected. Sand, gravel, and organic debris were present in all collections of anchor ice. Particles were not restricted to the bottom surface of the ice but were also observed within it. No particles over a quarter inch in diameter were observed and most of the material was sand.

Organisms collected included species of *Ephemerella, Glossosoma, Hydropsyche, Simulium* and *Elmis* (Table I). The mean number collected per square foot sample was ten. All insects collected were in the larval stage except for two adult *Elmis*. Inasmuch as drifting anchor ice could have considerable influence on the downstream transportation of bottom materials and organisms, drift samples were also collected with the sampler net and melted. No attempt was made to analyze drift samples quantitatively. Samples of drifting anchor ice showed the same materials and fauna as that in ice from the stream bed, plus *Chironomus, Antocha, Rhyacophila, Chimarra,* and one trout fry in the yolk-sac stage (Table I). The number and type of organisms collected in drifting anchor ice did not vary with time of day that the ice was released from the stream bed. All insects collected in anchor ice, both on the stream bed and drifting, were alive, but the trout fry was dead.

TABLE I. *Number and kind of organisms collected in anchor ice from the Pigeon River, Otsego County, Michigan, from Nov. 26, 1951 to Mar. 7, 1952*

	Collected from anchor ice on stream bottom				Collected from floating anchor ice				
Date of Collection	Nov. 26 1951	Jan. 4 1952	Feb. 15 1952	Mar. 6 1952	Jan. 4 1952	Feb. 15 1952	Feb. 17 1952	Mar. 6 1952	Mar. 7 1952
No. of square foot samples collected on stream bottom	1	1	3	5					
Oragnisms Collected:									
Annelida	1	..	..	..	..	..	..	..	1
Plecoptera									
Perlodidae	5	..	5	2	..	..	1	..	1
Ephemeroptera									
Ephemerella	3	3	1	2	1	..	5	4	29
Trichoptera									
Rhyacophila	..	..	..	..	1	..	..	2	1
Hydropsyche	2	1	10	2	..	4	1	3	61
Glossosoma	..	1	2	..	1	3	1	..	6
Chimarra	..	..	..	..	..	1	1		
Diptera									
Chironomus	..	..	..	..	..	1	1	1	2
Simulium	..	..	3	3	..	..	1	1	3
Antocha	..	..	..	..	1	..	1	..	
Coleoptera									
Elmis, adult	..	..	1	..	..	1	..	..	..
Elmis, larva	..	..	..	1	1	2	..	..	1

Influences of Anchor Ice on Stream Ecology

Much trout spawning had been observed in the same locality where anchor ice formed. Trout eggs were buried in gravel, however, and were below the influence of anchor ice. Trout fry in the egg-sac stage were vulnerable at the time of emergence and considerable mortality could be inflicted on sac fry if ice formed

[1] Contribution from the Institute for Fisheries Research, Ann Arbor, Michigan.

during the emerging period. It is doubtful if anchor ice could smother trout eggs because this ice condition seldom persisted over 12 hours and because the ice had a porous texture. Also, atmospheric conditions which were apparently necessary for the formation of anchor ice did not occur often on the Pigeon River. In many parts of the stream, anchor ice formation was restricted to early winter (Dec. 1-15) and late winter (Mar. 1-15) since surface ice prevented anchor ice formation for a long period in mid-winter.

The flooding caused by release of anchor ice dams altered the stream bed to a minor extent, but normal spring flood water was of greater volume and was observed to be of greater consequence in altering the stream bottom.

Maciolek and Needham (1952), state that anchor ice caused the dislodgement of bottom organisms and made more food available for trout. Sampling of trout populations on the Pigeon River in winter showed that all trout were in quiet eddies and under the banks. They were not feeding actively and coefficient of condition was low (Cooper 1953). Leonard (1942), after conducting winter trout stomach analyses on Hunt Creek, Michigan, questioned whether trout actually benefit much from winter feeding. The value of making food available to trout in winter is, therefore, questionable.

Although Brown *et al.* (1953) could not detect any appreciable change in numbers of bottom organisms where anchor ice formed, they do state that bottom organisms could be dislodged and carried away. In the Pigeon River the ice does serve as a method for downstream dispersal of bottom organisms. The small number so transported would never be sufficient to depopulate the stream bottom where ice was formed.

Summary

Observations were made on the Pigeon River, Otsego County Michigan, during the winter of 1951-52 to determine the influences of anchor ice on stream ecology.

Anchor ice formed during clear nights when the air temperature fell below minus 15.6°C. It formed most commonly in shallow turbulent water and usually floated away within 10 hours after its formation.

Samples of anchor ice on the stream bottom contained an average of 10 organisms per square foot plus sand, gravel, and organic debris. Floating anchor ice contained similar materials and fauna. All organisms collected were alive except for one dead trout fry in the egg-sac stage.

Anchor ice formed temporary retaining dams on the stream bottom but the resultant flooding was not observed to significantly scar the stream bottom.

This ice did serve as a method for downstream dispersal of bottom organisms. The small number so transported would not be great enough to deplete the bottom fauna population.

References

Barnes, H. T. 1928. Ice Engineering, Montreal: Renouf Publishing Co. 364 pp.

Brown, C. J. D., W. D. Clothier, and W. Alvord. 1953. Observations on ice conditions in the West Gallatin River, Montana. Proc. Mont. Acad. Sci., 13: 21-27.

Cooper, E. L. 1953. Periodicity of growth and change of condition of brook trout (*Salvelinus fontinalis*) in three Michigan trout streams. Copeia, **1953**: 107-114.

Hazzard, A. S. 1941. The effects of snow and ice on fish. Proceedings Central Snow Conference, Michigan State College, East Lansing, Michigan. Dec. 11 & 122, 1941, 1: 90-94.

Hubbs, C. S., and Milton Trautman. 1935. The need for investigating fish conditions in winter. Trans. Amer. Fish. Soc., **63**: 51-56.

Leonard, J. W. 1942. Some observations on the winter feeding habits of brook trout fingerlings in relation to natural food organisms present. Trans. Amer. Fish. Soc., **71** (1941): 219-227.

Maciolek, J. A., and P. R. Needham. 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California. Trans. Amer. Fish. Soc., **81** (1951): 202-217.

Needham, Paul. 1938. Trout streams. Ithaca, N. Y.: Comstock, 243 pp.

Surber, E. W. 1938. Rainbow trout and bottom fauna production in one mile of stream. Trans. Amer. Fish. Soc., **65** (1937): 193-202.

Norman G. Benson

Tennessee Game and Fish Commission,
Nashville 3, Tennessee

CONDITIONS FOR POPULATION EQUILIBRIUM[1]

It is possible to state the conditions which must be met by a population composed of a single species of animals (living in a constantly renewed environment, in the sense of Smith, 1952), if that population is to reach equilibrium. It is likely that numerical fluctuations of species that fail to meet these conditions are at least partially "internal" (in the sense of Slobodkin, 1954a).

The items of information necessary for determining whether or not the conditions for equilibrium are met follow:

I. Survival rate for animals of each age under varying conditions.

II. Reproductive rate for animals of each age under the same conditions.

III. Amount by which each animal of each age crowds the population (Andrewartha and Birch 1954) or contributes to population density (Slobodkin 1953b).

IV. Form of the density interaction (that is, the way in which total population density, D, is computed, given the density contribution of each animal and the number of animals in each age category).

V. Form of the dependence of reproductive rate and survival rate on population density.

I hold the concepts of "crowding" and "population density" to be essentially equivalent. The concept of D and of the form of dependence of reproductive rates and

[1] Contribution from the Department of Zoology, University of Michigan. This study was partly supported by research grants from the Conservation Foundation and the New York Zoological Society, while Visiting Investigator at the Bingham Oceanographic Laboratory, New Haven, in 1953.

survival rates on D are discussed somewhat more fully in Slobodkin, 1953b.

Consider a population divided into t age-categories, each of arbitrarily short time duration. It is assumed that all animals in a single age-category are physiologically identical. The animals born during a particular time interval, of the same duration as the interval spent in one age-category, will be designated n_0 and are assumed to make their first contribution to population density during the subsequent time interval. Animals born during a particular time interval will be designated as n_1 during the subsequent time interval. It is assumed that n_0 at time T is equal to n_1 at time $T+1$; that is, no mortality occurs in the transition from the 0th to the 1st age-category. For all age-categories older than the 0th it is assumed that a certain percentage of the animals die during the transition to the next older age-category. That is, if s_i is the survival rate of the animals of age i at time T, the number of animals in age-category $i+1$ at time $T+1$ is equal to $s_i n_i$. Survival rates are assumed to vary with the age of the animals and with environmental conditions, considering population density to be part of the environment of each animal.

If equilibrium is defined in its most stringent form it is equivalent to stating that both total population size and relative number of animals in each age-category remain constant with time. Births and deaths are equal during any time interval and are constant. For fuller discussion of this concept of equilibrium see Slobodkin, 1953b.

The number of young animals produced by an animal of age-category i, while in that age-category, is denoted by b_i which, like survival, varies with the age of the parent animal and with environmental conditions in the above sense.

In such an equilibrium population it can be shown that the following equation must hold:[2]

$$(a) \quad n_0 = \sum_{i=1}^{i=t} b_i n_i$$

Each n_i is equal to $s_{(i-1)}n_{(i-1)}$, the survivors from the next youngest age-category. In particular:

$$n_2 = s_1 n_1$$

so that

$$n_3 = (s_1 s_2) n_1,$$

or in general

$$(b) \quad n_i = (s_1 s_2 s_3 \cdot \cdots \cdot s_{(i-1)}) n_1$$

That is, at equilibrium any n_i can be replaced by n_1 times a product of survival rates.

We have already assumed

$$(c) \quad n_0 = n_1$$

We substitute the appropriate form of (b) for each n_i in (a) in order to put (a) in the notation of n_1 times survival rate products:

$$(d) \quad n_0 = \sum_{i=1}^{i=t} b_i (s_1 s_2 s_3 \cdot \cdots \cdot s_{(i-1)}) n_1$$

Dividing equation (d) by n_1 we obtain:

$$(e) \quad 1 = \sum_{i=1}^{i=t} b_i (s_1 s_2 s_3 \cdot \cdots \cdot s_{(i-1)})$$

which is identical with equation (1).

$$(1) \quad \sum_{i=1}^{i=t} b_i (s_1 s_2 s_3 \cdot \cdots \cdot s_{(i-1)}) = 1$$

In principle, the sum of products

$$\sum_{i=1}^{i=t} b_i (s_1 s_2 s_3 \cdot \cdots \cdot s_{(i-1)})$$

can be evaluated under any given set of environmental conditions. We will abbreviate this sum of products as G, which can be thought of as the increase potential of the population (this is almost identical with "growth potential" as defined by Boulding, 1954). If G is greater than 1 under a particular set of environmental conditions, it implies that if those conditions persist for a sufficient length of time the number of animals increases. Similarly if G is less than 1 for a sufficient length of time the population will decrease and if G is equal to 1, equilibrium is possible under the given conditions.

The stipulation of a "sufficient length of time" is necessary since the evaluation of G assumes an equilibrium age-structure. (This is not the same as the stable age distribution of Lotka, 1925; the distinction is treated at length in Slobodkin, 1954b). The greater the deviation from the equilibrium age-structure and the greater the physiological difference between members of different age-categories, the longer will be the time period, under any given conditions, during which the population history will deviate from that predicted by an evaluation of G.

A point which has received very little attention is that the range of conditions over which G equals 1 for any particular species may be very narrow or non-existent. It has been widely assumed that given any set of constantly renewed conditions which permit the species in question to survive, any population of that species will eventually produce an equilibrium in the above sense. More recently, experimental situations have been found for certain species in which, despite environmental constancy, no equilibrium is achieved. These have usually been dealt with as particular cases and as a rule the reasons for the absence of equilibrium are inferred after the experiments have been completed. It seems possible to predict the non-existence of equilibrium in populations of a particular species by evaluating G for a sufficiently wide range of conditions. If the environment is held constant experimentally, the only interesting variable condition the animals are subject to is their own population density. Evaluation of G under varying conditions of density may in some cases be easier than running long term population history experiments. If it is found that G, as a matter of fact, never does equal 1, or that the range of densities in which G is approximately equivalent to 1 is very narrow it may safely be predicted that population fluctuations will always occur in the species in question and that these will be at least partly internal, both in nature and in the laboratory.

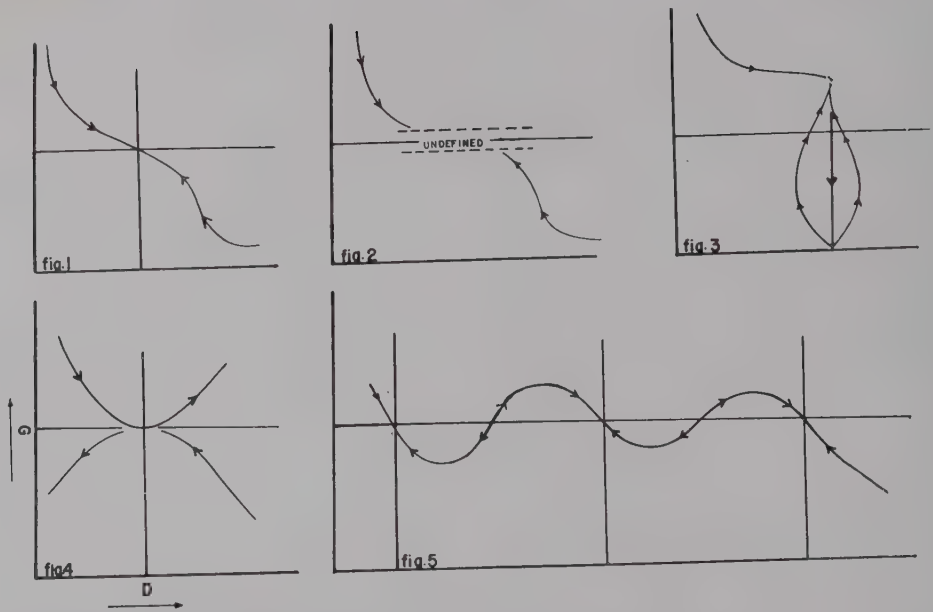
I can visualize five forms of interaction between G and population density which will account for all possible cases, so that any species can be fitted into one of the five categories.

1. There exists some value of population density, below which G is greater than 1, above which G is less than 1, or in the immediate vicinity of which G is not significantly different from 1 (Fig. 1). This is the case in which equilibrium in the laboratory is possible and fluctuations in nature are most likely under environmental control.

2. The value of G skips the region immediately around

[2] The demonstration follows:

The number of animals born during a particular time interval is equal to the sum of the products of the age-specific reproductive rates and the number of reproductive animals:



FIGS. 1-5. All possible relations between G and population density are indicated. These are enumerated and explained more fully in the text. The arrows indicate the direction of population change, if the populations have the age structure implied in the definition of G. Vertical lines in Figure 5 indicate density values at which stable equilibria occur. $G = 1$ is drawn as a horizontal line.

G-equal-to-1 (Fig. 2). This might be due to some discontinuity in the dependence of the reproductive rates or the survival rates on population density. It may not exist biologically but is included for the sake of completeness. In this case continual small scale oscillations would occur around the region of G-equal-to-1.

3. The value of G goes discontinuously from some value greater than 1 to 0 (Fig. 3). This implies a critical density value above which reproduction stops entirely. It seems very likely that many insect populations approximate this situation (Nicholson 1954). Species in this category will fluctuate in a constant environment and probably must rely on rapid migration and a high value of their intrinsic rate of natural increase for survival in nature (Andrewartha and Birch 1954, and references cited there).

4. (a) It is conceivable that for some populations G will be equal to 1 at some unique density and be less than 1 both at higher and lower population densities. Any slight disturbance of population equilibrium will cause the population to become extinct (Fig. 4).

(b) There may be a unique population density at which G equals 1, with G being greater than 1 both above and below this density. Any disturbance of an equilibrium population in this category will cause it to enter oscillations of the sort found in category 3, since it is clear that G cannot be greater than 1 for all high values of population density (Fig. 4).

5. It has been shown previously that if the form of the density interaction between the animals of a population is of third order or higher, optimal density effects will occur (Slobodkin 1953a). In the present symbolism this would involve two or more potential equilibrium points for the population. These equilibrium points will be alternately stable and unstable as density increases. Disturbance of a population at an unstable equilibrium point will result in shifting it to the next higher or next lower equilibrium point, which will be stable (Fig. 5).

The usefulness of the above relations is indicated below. In an analysis of population fluctuations in nature there is the omnipresent difficulty of distinguishing between internal and environmentally determined oscillations (Slobodkin 1954b). The only escape from the problem seems to be to determine the likelihood of internal oscillations on grounds which are independent of the actual field census. This permits some estimate of the degree of correlation that is to be expected between varying environmental conditions and the observed population fluctuations. The greater the expected internal oscillations, the lower the expected correlation with environmental changes, although small environmental changes might well trigger fairly extreme population fluctuations. Whereas it is obvious that the average value of G over an extended period of time must equal 1, unless the species is becoming extinct, as pointed out by Haldane (1953) and others, it is not necessary to assume that G is equal to 1 for any particular species during any particular short time interval, or for that matter that G is ever actually equal to 1.

The foregoing discussion has analyzed the various possible relations that may exist between G and population density in the absence of environmental fluctuations. It is to be expected that species which would show fluctuations due to interaction with their own population density alone will show more complex fluctuation patterns in a changing environment than those which will come to equilibrium in a constant environment.

References

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Chicago: University of Chicago Press, 782 pp.

Boulding, K. E. 1953. Toward a general theory of growth. Canadian J. of Econ. and Poli. Sci., **19**: 326-340.

Haldane, J. B. S. 1953. Animal populations and their regulation. New Biology, **15**: 9-24.

Lotka, A. J. 1925. Elements of physical biology. Baltimore: William and Wilkins, 460 pp.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian J. Zool., **2**: 9-65.

Slobodkin, L. B. 1953a. On social single species populations. Ecology, **34**: 430-434.

———. 1953b. An algebra of population growth. Ecology, **34**: 513-519.

———. 1954a. Population dynamics in *Daphnia obtusa* Kurz. Ecol. Monogr., **24**: 69-88.

———. 1954b. Cycles in animal populations. Am. Sci., **42**: 658-660, 666.

Smith, F. E. 1952. Experimental methods in population dynamics, a critique. Ecology, **33**: 441-450.

L. Basil Slobodkin

Department of Zoology
University of Michigan
Ann Arbor, Michigan

FLUCTUATIONS OF ANIMAL POPULATIONS, AND A MEASURE OF COMMUNITY STABILITY[1]

Fluctuations

Consider a food web as in Figure 1. This is interpreted to mean that S_1 eats S_2 and S_3, S_2 eats S_3 and S_4, and S_3 and S_4 rely upon a food supply, *i.e.* a source of energy, not shown.

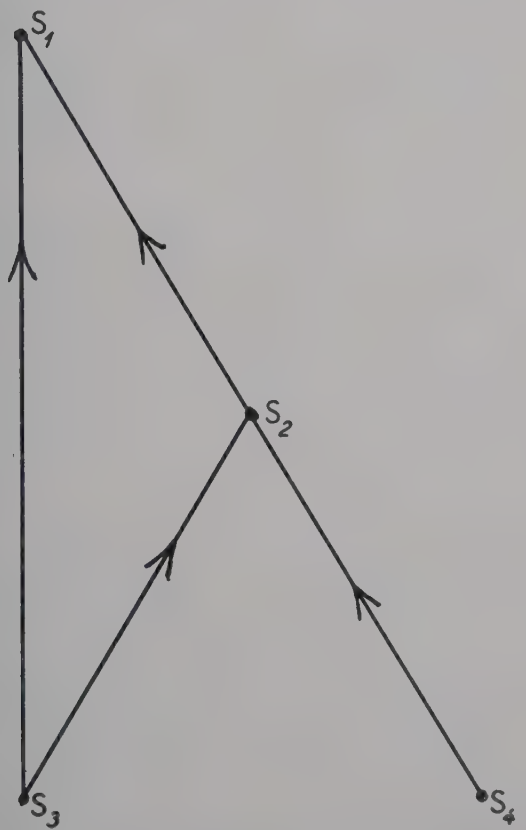


Fig. 1. A sample food web. S_1, S_2, S_3, S_4 are species, and arrows indicate direction in which energy flows.

[1] Contribution from the Osborn Zoological Laboratory, Yale University, New Haven, Connecticut.

Three assumptions will be made and a conclusion will be deduced from these. Since the conclusion is not always correct, it will be justifiable to conclude that one or more of the assumptions is responsible. First, temporarily assume that the amount of energy entering the community (at the lowest trophic level, of course) does not vary with time. Second, assume that the length of time that energy is retained by a species before being passed on to the next doesn't change from time to time. For example, if the animals die young in some year, this would violate the assumption. Third, assume that the population of each species varies directly with the food energy available. If a species first overeats and then starves (essentially a predator-prey reaction) or follows changes in available energy only after a time lag, then this assumption is violated.

These three assumptions imply that the population of each species tends to a specific constant, independent of the initial populations of the species. Proof: Since no species is perfectly efficient at transferring energy from its prey to its predators (Lindeman 1942), energy leaves the web from each species, and in view of the assumptions the amount of energy leaving equals that entering. This is then equivalent to saying that the energy leaving the community is the energy which reenters. That is, the consequences of this will be identical. This energy can now be entered on the food web of Figure 1 as S_5 and it now looks like Figure 2. Let p_{ij} be the proportion of the energy of S_i which goes to S_j. Since all of the energy transferences are shown.

$\Sigma_j p_{ij} = 1.$

This equation shows that the food web considered as an energy transformer is what is known in probability theory as a Markov chain (Feller 1950). Furthermore, if the number of links in a complete cycle of the energy is called the length of the cycle, the greatest common divisor of these lengths is 1 and so the conditions set forth in Shannon and Weaver (1949) for the Markov chain to be "ergodic" are satisfied. Therefore, as shown in Feller (1950), the amount of energy at each point tends toward a constant, independent of the initial conditions. In view of the assumptions, the species populations also approach constant values. This completes the proof.

Since populations of species often fluctuate in nature, it can be concluded that one or more of the three assumptions is failing to hold. Furthermore, it is clear from the theorem that the structure of the food web cannot

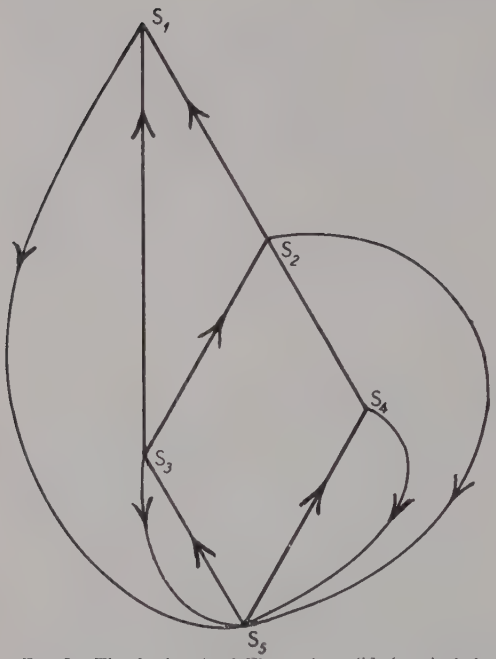


FIG. 2. The food web of Figure 1 modified to include lost energy.

be responsible for fluctuations. Therefore, an explanation of the fluctuations must lie in predator-prey relations, time lag phenomena, or other violations of assumption three; in environmental variations in available energy, violating assumption one; or in variations in age at death, violating assumption two.

COMMUNITY STABILITY

In some communities the abundance of species tends to stay quite constant, while in others the abundances vary greatly. We are inclined to call the first stable and the second unstable. This concept can be made more precise, however. Suppose, for some reason, that one species has an abnormal abundance. Then we shall say the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community.

This stability can arise in two ways. First, it can be due to patterns of interaction between the species forming the community; second, it can be intrinsic to the individual species. While the second is a problem requiring knowledge of the physiology of the particular species, the first can be at least partially understood in the general case. Only this kind of stability will be considered here.

The interactions between species are represented graphically in a "food web" of the community, in which "a eats b" is represented by

$$\begin{matrix} a \\ | \\ b \end{matrix}$$

with the predator above the prey. Energy goes from b to a in this process. More generally it passes from the sun to the lowest trophic level and thence up through the web to the highest level of carnivore. A qualitative condition for stability can now be stated. The amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community (Odum 1953). To see this, consider first a community in which one species is abnormally common. For this to have a small effect upon the rest of the community there should be a large number of predators among which to distribute the excess energy, and there should be a large number of prey species of the given species in order that none should be reduced too much in population. To sum up, a large number of paths through each species is necessary to reduce the effect of overpopulation of one species. Second, suppose one species is abnormally uncommon. For this to have minimum effect upon the rest of the community, each predator of the species should have a large number of alternate foods to reduce the pressure on the scarce species and yet maintain their own abundance at very nearly the original level. There is good evidence for this in Lack (1954). We see that in either case the amount of choice of the energy in going through the web measures the stability.

A difficulty arises in making this definition quantitative, because our intuition of what stability means is ambiguous. For the concept "effect upon the other species of the community" required in the definition can be interpreted in many different ways. It could be the average (over all species) maximum change in abundance, or the relative changes, or mean square changes, or different species could be weighted differently, etc. The intuitive requirements seem to be that if each species has just one predator and one prey the stability should be minimum, say zero, and that as the number of links in the food web increases the stability should increase.

One further (arbitrary) requirement will specify the function, however. For proof, see Shannon and Weaver (1949). The most convenient requirement is that the stability of two webs such as in Figure 3 and Figure 4 should be equal. Here the ½'s between ab and ae signify that each of b and e is an equally possible food of a (*i.e.* $\frac{1}{2} + \frac{1}{2} = 1$). Now energy has complete freedom of choice to go to a from section bcd or from section efg. Hence if $S(abe)$ refers to the stability of abe considered as a separate community, etc., it is reasonable to define the stability of the whole web in Figure 3 as $S(abe) + \frac{1}{2}\, S(bcd) + \frac{1}{2}\, S(efg)$. If we say that this should be equal to $S(a'c'd'f'g')$ in Figure 4, the appropriate stability function is

$$S = -\sum p_i \log p_i$$

where the p_i are the numbers in Figure 4. (*E.g.*, for either the web of Figure 3 or of Figure 4 the stability is $-4(\frac{1}{4} \log \frac{1}{4}) = \log 4$). To find the stability of any web, construct an equivalent one by making a separate line from top to bottom for each different path the energy can take. The p_i in the definition are the products of the q_i of the original web along each path. It may be significant that this is identical in form to the functions measuring entropy in Maxwell-Boltzmann statistics and information in information theory (Shannon & Weaver 1949). Entropy is also analogous in the sense that maximum entropy is the condition for chemical equilibrium while maximum stability may be a condition for community equilibrium (Hinshelwood 1951). It should be pointed out that choice among various functions to define stability precisely rests only upon usefulness of the definition (provided of course that the intuitive conditions mentioned above are satisfied).

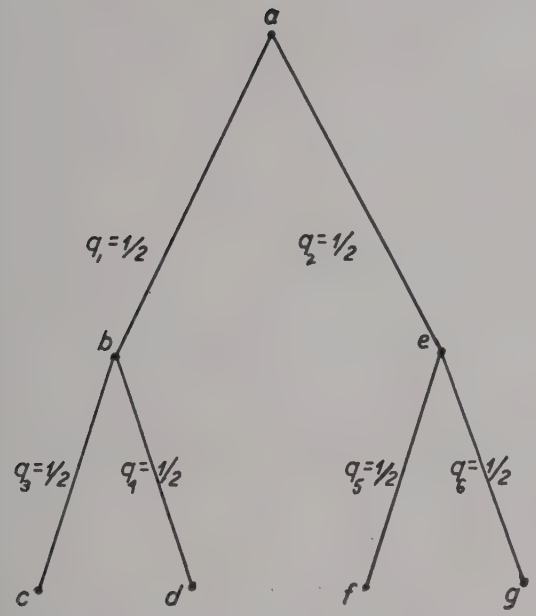


FIG. 3. A food web. *a*, *b*, *c*, *d*, *e*, *f* and *g* are species, and *q* on the line joining predator and prey signifies that fraction of the total number of prey species formed by the prey species in consideration.

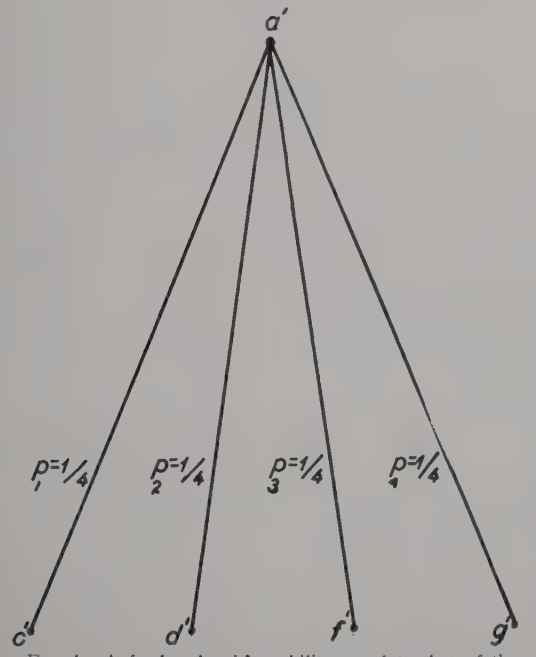


FIG. 4. A food web with stability equal to that of the food web in Figure 3.

There are several properties of this stability which are interesting.

1. Stability increases as the number of links increases.

2. If the number of prey species for each species remains constant, an increase in number of species in the community will increase the stability.

3. Combining 1 and 2, it follows that a given stability can be achieved either by large number of species each with a fairly restricted diet, or by a smaller number of species each eating a wide variety of other species.

4. The maximum stability possible for m species would arise when there are m trophic levels with one species on each, eating all species below. Similarly, the minimum stability would arise with one species eating all the others—these others being all on the same trophic level. (These are plotted in Figure 5.)

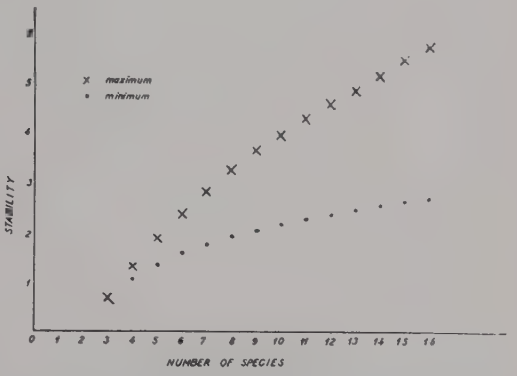


FIG. 5. Maximum and minimum stabilities for a given number of species. All communities must have stabilities within these limits.

Some interesting conclusions may be drawn from these properties. First, (1) implies that restricted diet lowers stability. But restricted diet is what is essential for efficiency. Furthermore, efficiency and stability are the two features required for survival under natural selection. Efficiency enables individual animals to outcompete others, but stability allows individual communities to outsurvive less stable ones. From this it seems reasonable that natural selection operates for maximum efficiency subject to a certain necessary stability. Combining this with the properties listed above the following seem plausible.

A. Where there is a small number of species (*e.g.* in arctic regions) the stability condition is hard or impossible to achieve; species have to eat a wide diet and a large number of trophic levels (compared to number of species) is expected. If the number of species is too small, even this will not assure stability, and, as in the Arctic, populations will vary considerably.

B. Where there is a large number of species (*e.g.* in tropical regions) the required stability can be achieved along with a fairly restricted diet; species can specialize along particular lines and a relatively small number of trophic levels (compared to number of species) is possible. (The possibility that the large number of species in tropical communities may be a result of, rather than the cause of, the restricted diets would not alter the above argument.)

REFERENCES

Feller, W. 1950. An introduction to probability theory and its applications. New York: Wiley.

Hinshelwood, C. H. 1951. The structure of physical chemistry. London: Oxford.

Lack, David. 1954. The natural regulation of animal numbers. London: Oxford.
Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, 23: 399-418.
Odum, E. P. 1953. Fundamentals of ecology. Philadelphia: Saunders.
Shannon, C., and W. Weaver. 1949. The mathematical theory of communication. Urbana: Univ. Illinois Press.

ROBERT MACARTHUR

DW RANCH,
HEREFORD, ARIZONA

STUDIES FROM THE AUTOTREPHON, IV. REARING MASS CULTURES OF ORYZAEPHILUS

The autotrephon (Stanley 1951) requires very large cultures of insects, from which eggs are obtained for seeding the replicated samples. This is so because all the eggs used for a run, perhaps 2,500 of each species, must be obtained within a period of not more than say 2 hr. This presents no problem with *Tribolium* as very large cultures of this insect can easily be maintained in flour. In the cases of *Oryzaephilus surinamensis* and *mercator*, this is not so easily done. These insects do not tunnel to any extent. They use only the superficial layers of flour, and crowding occurs, with reduction of egg-production.

The writers have found that these insects can be grown in enormous numbers in ordinary rolled oats if precautions are taken to cope with the large quantities of metabolic water produced. Referring to Figure 1, the culture is set up in a 1-gallon glass jar with a 3-in. disc of 40-mesh stainless steel cloth set in the lid for ventilation. A cardboard washer, ¼ in. wide with a 3 in. hole is used to seal the lid (Fig. 2). About 2 in. of soft-wood shavings are poured into the jar, and another 2 in. of rolled oats poured on top. A suitable temperature is 30°C., but the relative humidity should not be above 60%, or water will collect on the sides and run down into the oats. Extreme moulding will then occur. The life-history requires about 650 hr. for *surinamensis* and about 700 hr. for *mercator*, and the culture lasts without serious moulding for much longer than this.

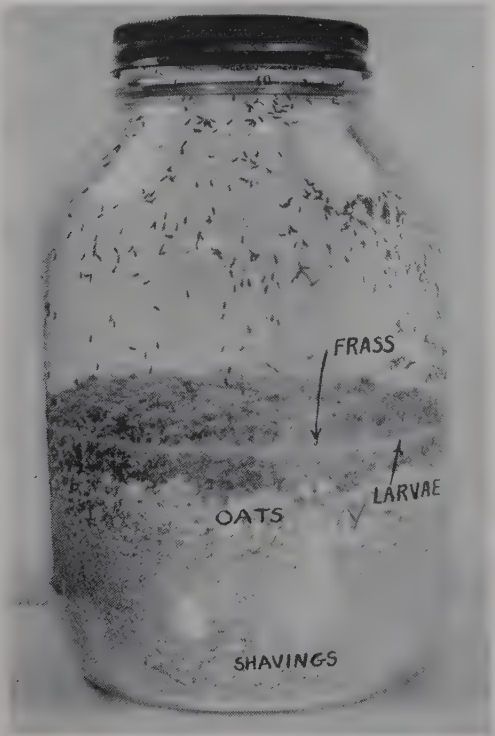


FIG. 1. A culture of *O. surinamensis*, with shavings at the bottom, rolled oats above this. Adults are climbing the glass, and larvae are trying to.

In Figure 1, the apparent dark layer on top is merely the shadow of the lights (which show as reflections on the shavings). A faint gray line marked "frass" is a mixture of frass and larval smearing, indicating the original level of the oats. The shavings are clogged with frass which has fallen into them. Numerous larvae can be seen trying to climb the glass at the top of the oats.

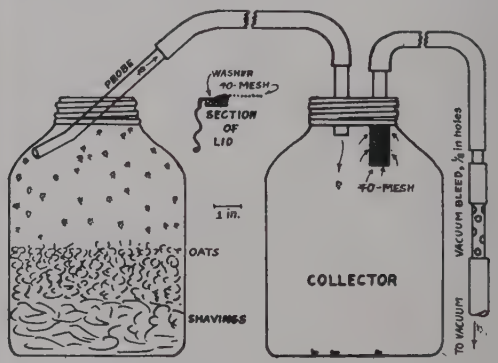


FIG. 2. Suction apparatus for removing *O. surinamensis* adults from a culture.

When disturbed, *O. surinamensis* climbs the glass in swarms, but *O. mercator* does not. It has been observed in this laboratory that if one considers a pair of similar kinds of insects, say *O. surinamensis* versus *O. mercator* or *Tribolium castaneum* versus *T. confusum* or even the red strain of *Tribolium* versus a black mutation (for either *castaneum* or *confusum*), the insect with the shorter life-history is always the more active. The first member of each pair above has the shorter history, climbs or flies more, and is more active and difficult to handle. The meaning of this is not clear, unless both characteristics be tied to higher basal metabolism.

A special technique is needed to get *O. surinamensis* into flour (siftable) for egg production. The writers

use a vacuum probe as shown in Figure 2. The suction line on the collector jar is connected to a vacuum cleaner, with a vacuum bleed interposed. Sliding the tube of the bleed further into the rubber tube covers some holes, and increases the suction. A 40-mesh sleeve covers the air outlet of the collector jar. If the suction is too great, the beetles are slammed to the bottom of the collector jar. This disturbs them so much that they will not lay for many days thereafter. We usually let them rest for at least a week in flour, before taking eggs.

O. mercator is much easier to handle. One sifts first with a coarse sieve (12 to 13 mesh, or "fly wire"). This holds back the oats and lets the adults through. A second sifting through 30-mesh holds back the adults but lets any bits of oats through. Any attempt to sift *surinamensis* in this way will necessitate a hurried call for the Headmaster of St. Trinian's. No one else could cope with the riot.

Acknowledgments

The writers are indebted to the National Research Council of Canada for financial support of this and related work with the autotrephon, and to the McGill Research Fund for other financial support. The apparatus was made by Mr. J. W. Pollock, Instrument Maker and Technician of the Department of Zoology, for whose interest and great skill the writers are long indebted.

Reference

Stanley, J. 1951. The autotrephon: an apparatus for rearing insects under controlled conditions with automatic time-controlled withdrawal of samples. Ecology, **32**: 413-442.

John Stanley
Sally J. Evans

Department of Zoology,
McGill University,
Montreal, Canada

REVIEWS

A New Non-elementary Book of Ecology[1]

In the last five years, following the publication of "Principles of animal ecology" by Allee, Emerson, Park, Park and Schmidt, ecologists have for the first time had the satisfaction of seeing textbooks dealing with their subject coming from the presses at an adequate rate. These books have facilitated the teaching of ecology but have had little significant impact on the thinking of ecologists. Now, it seems, the non-text books of ecology, intended to influence the thinking of ecologists, are also starting to appear. The present volume by two Australian scholars is of this type and is probably the most significant ecological book to appear since the publication of Allee *et. al.*

This book is about as large as, and even more expensive than "Principles of animal ecology" but its scope is far narrower. It does not deal at all with the history of the subject nor with communities, it does not deal with soil profiles, meteorology, or many other familiar features of the recent texts, and the taxonomic range of the examples is decidedly limited. Nearly all aspects of plant ecology are explicitly ignored and a casual reader might get the impression that the word "animals" in the title means "insects," or even "thrips, grasshoppers, and stored-grain insects," the discussion of which must occupy something approaching one-half of the book. This book, however, is not for the casual, as the authors explicity assume of the reader a working knowledge of statistical procedures and a considerable background in ecology and an acquaintance with ecological literature (e.g. "The migrations of certain birds and fishes are too well known to need recapitulation here. . . ." p. 116). Those who actually read the book will probably not object to the effort to develop general principles from the detailed consideration of highly specific examples.

This entire book, culminating in what the authors call ". . . . a wide and satisfying general theory of ecology . . . ." (p. 5) is built around one simple recurring theme which presents distribution and abundance as two aspects of the same phenomenon. In the authors' words (p. 9): "For the numbers of an animal present in an area are determined by the animals' chance to survive and multiply. This is limited by the environment. As the severity of the several components of environment which impose the limitation increases, the numbers decrease, eventually becoming zero as the limits of the distribution are reached." This theme may be seen to be a probabilistic interpretation of survival and multiplication in which environmental factors, including climate, govern the probability of success in reproduction, and population size naturally follows this probability distribution. This seems to be precisely V. E. Shelford's "law of toleration" expounded in 1911 in a paper not cited by Andrewartha and Birch (Jour. Morp. 22:599), and modernized by introducing the concept of probability ("chance"). It is today so commonplace to interpret the observed frequency of an event as an expression of an underlying probability of occurrence of the event that present-day scientists are unlikely to object to the authors' probabilistic approach. Hence, this theme seems to be an eminently sensible one with which to approach the study of ecology.

This, however, is an iconoclastic book and the authors will be accused of developing their theme for an accompaniment of firearms. In their approach to ecology there is no need for density-dependent factors to halt unlimited population growth or decline, and an alternative classication of ecological factors into "biotic" and "physico-chemical" is also rejected as unnatural. In discussing the ecology of a species they view other species as a part of the environment and so relegate to "competition" an extremely minor role. Similarly, a population is part of the environment of the individuals so that the concept of the supraorganism is neglected. The Van't Hoff and Arrhenius temperature equations are demolished by p. 147; the method of temperature summation is smashed by p. 162; the concept of "bound water" as a factor in low temperature toleration is demolished on p. 196; the "saturation-deficiency law" is pretty well shot up by p. 256; beginning at about p. 348 a virtual barrage is loosed at the logistic model of population growth; the generalization that "two species with identical ecological niches cannot survive together in the same environment" is a frequent target; mathematical models of specific interactions are attacked in general, but special aim is taken at the theories associated with the names of Lotka, Volterra, Nicholson and Bailey; and the authors even go so far as to "suggest that natural populations rarely consume a large proportion of the food available to them." (p. 464). These are just examples of widely accepted generalizations, some of which have nearly achieved the status of axioms, which Andrewartha and Birch have called into question. Their skepticism is thoughtful and objective and certainly one major importance of this volume will be the stimulus for re-examination of many basic assumptions. However, when two skillful marksmen direct their aim at so many targets they are certain to be accused of being trigger happy. This book will unquestionably provoke repercussions and the reviewer cannot leave the subject of iconoclasm without looking a little more closely at some of the authors' major criticisms.

Probably no other single point in this book is reemphasized so often as the "fallacy" of classifying the environment into "density-dependent" and "density-independent" components. The reviewer has also criticised this classification as useless, misleading, and, in agreement with the present authors, on the grounds that no component of the environment is conceivably density-independent. In beginning to read this volume the reviewer was first pleased with the authors' attitude, then impressed with the fact that they must continually have had to defend their viewpoint against colleagues. Eventually the reviewer began to feel that the authors were "beating a dead horse" or setting up straw-men to demolish. Could the dogma of "density-dependent" factors actually lead anyone to say something like "Because an insecticide is not a density-dependent factor, it cannot regulate the numbers in a population" (p. 662)? Examination of another new book on populations and re-examination of some papers cited by Andrewartha and Birch suggests that the danger is real; this dogma is more confusing than the reviewer had suspected. On this and on numerous other points such as their criticisms of the competition and predation equations, the authors are to be congratulated for their iconoclasm.

The authors' continual criticism of "competition" as a

[1] Andrewartha, H. G., and L. C. Birch 1954. The distribution and abundance of animals. xv + 782 pp., 214 figs. Chicago: University of Chicago Press. $15.

factor controlling population density merits careful study. It is obvious that the word "competition" has been misused (cf. p. 23 seq., p. 205), or rather used in numerous and sometimes contradictory ways, so that one may object to it on semantic grounds. This, however, is not the main point made by Andrewartha and Birch. After considerable reflection the reviewer concludes that their main point is well taken; competition operates primarily in determining *which* individuals or species survive, not *how many*. This is certainly a controversial and stimulating point and the arguments should be examined by all professional ecologists.

Only rarely do the authors raise criticisms which can be reduced to semantic quibbles. Their above-mentioned conclusion that populations seldom consume a large portion of the available food appears to be an attack on a basic tenet of ecology which is supported by the obvious facts that food resources show no tendency toward continuous accumulation and that populations have often been stimulated to increased growth by the provision of additional food. Here, however, the real quarrel seems to be over the definition of the word "available."

The authors' extensive criticism of the logistic curve as a representation of population growth is somewhat unfortunate, for they admit its value as an empirical representation for this and other purposes but add an erroneous criticism to the stock of oft-repeated criticisms. They incorrectly state (several times) that it is implicit in the logistic theory that the age distribution of the population should remain unaltered throughout its growth. This misconception arose from imputing too much generality to a model studied by Leslie in which he showed that a population can grow logistically with a stable age distribution *if the life table is continuously changing*. Unfortunately, Andrewartha and Birch overlooked an important 1931 paper by Lotka (Human Biol. 3:459) in which he showed that a population can grow logistically with a fixed life table, but *in this case the age distribution changes continuously* and systematically with time. It is, in fact, easy to show that a growing population with both a fixed life table and an unvarying age distribution cannot exhibit sigmoid growth of any sort, it must grow exponentially. Actually, the case with an unchanging life table (constant age-specific death rates) should have greatly interested the authors in connection with their general viewpoint. Leslie's case seems more consistent with "density-dependent" controlling factors and, furthermore, Skellam has recently published (Biometrika 38:215)[2] a most interesting logistic model in which two species competing for the identical niche requirements can co-exist indefinitely. It is unfortunately that this incorrect criticism of the logistic formula partially invalidates the authors' criticisms of the competition equations which are the basis for the conclusion that species cannot co-exist in total competition.

To this point we have dealt largely with the demolishinary aspects of this book; it has, however, equally valuable constructive aspects. The examples, which are heavily weighted toward experimental and entomological literature, have been carefully extracted from a large number of sources, many of which have not been cited in previous books of ecology. Hence the 41 page combined bibliography and author index is a valuable contribution in its own right.

[2] The review editor expresses hearty approval of the practice of calling attention to important publications other than those actually being reviewed.

The authors' statistical leanings have led them to several approaches not found in other books of ecology. Outstanding in this connection is their introduction of some of the newer methods of bio-assay analysis into the discussion of toleration physiology (p. 178 seq.). While this is a natural enough thing to do, a real contribution has been made by bringing these techniques to the attention of ecologists. Their discussions of dispersal, population growth, the "innate capacity for increase in numbers" (= intrinsic rate of natural increase), and similar matters is, as we might anticipate, unusually lucid and sound, with minor exceptions. The "approximate" calculation of innate capacity illustrated on pp. 41-42 is generally so poor that it can scarcely be called an approximation, and, as suggested earlier, the authors have succeeded in introducing some confusion into the concept of the stable age distribution. Multiple and curvilinear regression methods are introduced in discussing a paper by Davidson and Andrewartha which, in the original, probably occupied no more space than it is allotted in this book (Fig. 6.08 on p. 143 and Fig. 13.04 on p. 573 are identical, and come from this paper). Multiple regression is a tricky subject and strange results are possible when, for example, the "independent variables" are not really independent. This is one of the very few places where the reviewer felt that the authors' critical capacities were below their usual level.

Space limitations make it impossible to attempt any inventory of the important features of this large and valuable book. It is organized into five principal sections as follows: 28 pages of basic concepts entitled "introduction," 93 pages on the "physiological aspects of ecology," 416 pages entitled "analysis of environment," 118 pages entitled "the numbers of animals in natural populations," and 56 pages on "the genetic aspects of ecology." This last section appears to be nearly independent of the remainder of the text and one wonders slightly why this material was not integrated into the other sections. Here the authors are more orthodox (genetically) than elsewhere and, disappointingly, they appear to be content with a species concept based on Mendelian populations and isolating mechanisms which are exclusively geographic. Since a general theory of ecology must be concerned impartially with plants and animals, and with asexual and parthenogenetic forms, and with situations where one must stretch his credulity to imagine geographic isolation, the reviewer found this section somewhat less satisfying than the corresponding part of Allee *et. al.*

The book is written in a beautifully clear style almost totally free of ambiguities and undefined terms and concepts. It is almost free of typographical errors and the reviewer found none that could conceivably be confusing. The format, binding, and paper are excellent and the many graphic illustrations are excellently reproduced. The authors have avoided the common pitfalls of finding adaptations by subjective means and they have avoided the common semantic pitfalls of defining such ways of life as predation and parasitism in terms of "harm" and "benefit." They have written an original, esoteric, iconoclastic, and provocative book which is a genuinely important contribution to the science of ecology and which must be on every ecologist's bookshelf.

LAMONT C. COLE

DEPARTMENT OF ZOOLOGY
CORNELL UNIVERSITY

The Vertebrates Through Time[1]

The substance of this excellent book by an acknowledged authority adheres well and truly to the title. Each of the successive vertebrate groups is followed from its origin to the emergence of the next more advanced group, and tracing of the intricate paths toward world conquest by these animals is unmarred by digressions and moralizings. Thus, the evolutionary pattern of the fishes is traced to the origin of the amphibians via the rhipidistians, the amphibians to the appearance of the cotylosaurian reptiles, and so on. Treatment of the various groups is even, and the primates are given the relatively few pages they deserve. There is special and satisfying emphasis on the slow and painful evolution of many of the commonplace structures of later vertebrates, often taken more or less for granted as "fundamental" by students, such as jaws, teeth, limbs, body coverings, and others.

The drawings and sketches by Lois Darling add much to the pleasure of reading this book. Unlike so many restorations of extinct organisms in recent texts, the animals in these look as if they really did live. Phylogenetic charts and diagrams of basic morphology are clear and uncluttered. An appendix outlines an up-to-date classification of the chordates, emphasizing the vertebrates.

It is difficult to find and ungracious to point out errors of fact in this book. The only obvious one noticed is the statement on page 81 that Ellesmere Land is in eastern Greenland. The origin of the vertebrates, still largely a matter of speculation owing to the paucity of the earliest vertebrates in the fossil record, is rather weakly dealt with, only *Amphioxus* being mentioned as representative of vertebrate beginnings, with no reference to other chordates and to the probable common origin of echinoderms and chordates, or to the intriguing implications of the carpoids.

For some years the reviewer has given a "cultural" course in geological life development dealing largely with the vertebrates. One difficulty has been a suitable textbook. Dr. Colbert's book fits the bill exactly for the vertebrates. Will someone kindly do something like this for the invertebrates?

[1] Colbert, E. H. 1955. *Evolution of the Vertebrates,* vii + 479 pp., 122 figs. New York: John Wiley. $8.95.

John W. Wells
Department of Geology
Cornell University.

The Behaviour and Social Life of Honeybees[1]

Many books have been written about bees since the classic writings of John Lubbock (1874). Therefore, it is a real achievement to produce another which is a scholarly treatment of the subject and a useful contribution to both workers and general readers in this field of study. Ronald Ribbands, Principal Scientific Officer, Bee Department, Rothamsted Experimental Station, Harpenden, England, has accomplished this in a book which summarizes previous work extensively and integrates it well with recent observations, particularly those of the author and his co-workers at Rothamsted as well as those of C. G. Butler, M. Lindauer, M. H. Haydak and Karl von Frisch. This book has the present, best answer to hundreds of questions about bees and with its extensive bibliography of nearly seven hundred references it will be a great aid to young investigators in finding a good subject for further research. It is well illustrated with instructive graphs and diagrams and nine plates of photographs which are excellent close-ups of various bee activities.

The book contains four parts. Part I, The Roots of Behaviour, deals with the kinds and amount of sensory perception possessed by bees, the role of glands, and the fundamental differences between workers, queens, and drones. Parts II and III describe the field behaviour, foraging and communication of bees concerning the source and gathering of pollen and nectar. This information is presented with special reference to its useful application in bee culture and the pollination of crops. Part IV is concerned with the complex activities and division of labor in the bee community. Here, both the applied and the general biological aspects of the remarkable adaptations are discussed at length. Especially interesting and significant to this reviewer are the sections dealing with food sharing, temperature regulation and caste differentiation as factors in the social organization of the bee community. Similarly every reader will find many items which are interesting or useful to himself.

[1] Ribbands, C. R. 1954. The Behaviour and Social Life of Honeybees. 352 pp., 66 figs., 9 plates. Hapeville, Georgia: Hale Publishing Company. $4.50.

William A. Dreyer
Zoology Department
University of Cincinnati

The Cultivation of Animal and Plant Cells[1]

A recent article with the intriguing title "Observations on the Social Behavior of Cells in Tissue Culture"[2] draws attention to the fact that real efforts are being made to develop ecology at the cellular level. It seems appropriate, therefore, for this journal to review Philip White's excellent little book on tissue culture. As the author points out, from a study of cells cultivated *in vitro* we may find answers to many of the perplexing problems concerning their ecological relations in the community of cells which is the organism. It is on this note, with

[1] White, P. R. 1954. *The Cultivation of Animal and Plant Cells.* xi + 239 pp., 54 figs. New York: The Ronald Press Co. $6.00.

[2] Exp. Cell Res. *6:* 293-306 (1954).

much reverence to the contributions of Dr. Philip R. White and others, that the author launches into his lucid descriptions of the methods employed in cell culture.

Since it is absolutely essential in cell culture that no toxic material come in contact with the living material, washing and sterilization of glassware has become extremely important. In many laboratories this procedure has developed into an unnecessarily complicated rite; the author has described several of the more simple means of overcoming this hurdle. His descriptions and illustrations of devices such as polishing blocks for cover slips are especially helpful for the beginner. Included in the first section of the book is a comprehensive list of essential and useful equipment for cell culture.

Rather than enter into an involved discussion of the theory of plant and animal cell nutrition, Dr. White has proceeded to the more practical side of the medium picture, i.e. appropriate solutions, formuli, and methods of preparation. One of the most useful sections of the book concerns the actual mechanism of setting up tissue cultures. The author takes the reader through several typical preparations including outlay of the necessary equipment, the mechanics of dissection, down to the final setting of the slides, tubes, or flasks into the incubator. His instructions are simple and easy to follow.

In his laboratory Dr. White has eliminated the use of surgical masks, gowns, table covers or special scrubbing beyond usual cleanliness, and has found that he has lost very few cultures from bacterial contamination. Applying this to my own work I have found his advice sound, and would heartily recommend this view of aseptic technique to anyone intending to use the method of cell culture.

The book contains extensive references, is well indexed, and serves as an excellent manual for someone interested in the basic "how to do it" aspect.

Let it not be said that the author has presented an oversimplication of the methods used in growing living cells. Rather, he has succeeded in his attempt to strip a complicated technique of its oftimes overwhelming aura of mysticism and complexity in order to make it easily available to a large number of workers.

Marcia J. Loeb
Department of Zoology
Cornell University
Ithaca, N. Y.

Symposium on the Acoustics of Orthoptera[1]

Among insects which use sounds for communication, the members of the Order Orthoptera, particularly the locusts and crickets, have been probably the most intensively studied. The work of the pre-recording era was often hampered by the absence of methods for isolating specific sounds and by lack of means of communication among the workers. The development of the modern tape recorder and of new instruments for analysis of sounds has opened the field to more precise scientific investigation. Students of sexual selection and speciation, and of comparative animal behavior can find many challenging problems in insect acoustics.

The book here reviewed indicates some of the problems and fruits of studies on insects of this one Order. It consists of 23 papers presented by French, German, British and American workers at a symposium held at Jouy-en-Josas, France, 5-8 April, 1954, under the leadership of R.-G. Busnel, Directeur du Laboratoire de Physiologie Acoustique de l'Institut National de la Recherche Agronomique. The papers were either originally in French or have been translated into that language for publication.

The book is divided into four sections. The first (7 papers) deals with definitions and fundamental concepts in acoustics, and with recording, reproducing and analyzing techniques useful for studies on insect sounds. The second section (10 papers) deals with the structure and action of sound-producing organs of Orthoptera, including both stridulatory and non-stridulatory types. The third section (6 papers) deals with reception of sounds and reactions to natural and artificial sounds by these insects. The concluding section is a bibliography of 1,175 titles on sound production and reception by insects in general.

Biologists thinking to use the new techniques for recording and projecting sounds should note especially the first section of this book. Microphones, recorders, amplifiers, loud-speakers—all have limitations. The understanding of the limitations and the correct use of equipment is essential if one is not to have merely pseudo-precision. A large and complicated piece of physical equipment with properties unknown to the biologist using it may be only an impediment to understanding. Not that this book offers answers to many acoustic problems; it only highlights the problems. Reading it should warn the biologist that "Hi-Fi" for the human ear or for specialized acoustic uses is not necessarily good enough for studies with insects that use frequencies above or below those perceived by man, and for which the temporal parameters of sounds, particularly the distribution of transients, may be so important. It is significant that this first section is presented almost entirely by acousticians and electronics specialists. Biologists planning to work in this field will find these experts indispensable.

The papers on production and reception of sounds by Orthoptera are of different lengths and coverage. Some are preliminary reports, others fairly detailed. They present, however, only a picture of current research. There is no complete or integrated treatment of the field. This must await the studies which are to come. The Symposium was designed to reveal current trends. It is too early in the work to do more than to present data and to suggest possible generalizations for future research to test.

Hubert Frings
Department of Zoology & Entomology
Pennsylvania State University

[1] Busnel, R.-G. (Editor), 1955. L'Acoustique des Orthoptères. 448 pp., Illus. Paris: Institut National de la Recherche Agronomique. 2.800 fr. ($8.00).

ANNOUNCEMENTS

The Southwestern Research Station of the American Museum of Natural History

The American Museum of Natural History has announced the establishment of The Southwestern Research Station. It is located on the eastern slope of the Chiricahua Mountains, near Portal, Cochise County, in southeastern Arizona. The property is within the limits of the Coronado National Forest at an elevation of 5400 feet.

The station was established for the purpose of making available research facilities for scientists and students in all branches of science, who have problems that can be investigated through the utilization of the faunal, floral and geological features of the area. It will be open during the entire year.

It is operated by the American Museum of Natural History, Central Park West at 79th Street, New York 24, New York and under the direction of Dr. Mont A. Cazier, Chairman and Curator of the Department of Insects and Spiders, to whom all inquiries should be addressed. Anyone interested in the station should write to the above named individual for the booklet which gives the details of the operation and a general description of the area.

Bulletin Signaletique d'Entomologie medicale et veterinaire

The *Bulletin Signalétique d'Entomologie médicale et vétérinaire* is a new bibliographic periodical for medical and veterinary entomology, published by l'Office de la Recherche Scientifique et Technique Outre-Mer, 20, rue Monsieur, Paris VII°. More than 200 periodicals published or received in France are covered. The Bulletin is divided into two parts. In one, articles are listed under the appropriate subject rubric (or rubrics): Culicidae, general; Anophelini and malaria; Culicini and yellow fever; Insecticides; Ecology and Biogeography, etc. These references are designed to be cut out and pasted on cards. No abstracts are provided, but new names of insects are given, as well as the names of insects mentioned in the texts but not in the titles of articles. In the second part the articles are listed according to the periodical in which they appeared, and annual indexes permit ready use of these lists.

Three numbers of Volume I appeared during 1954; beginning with Volume II, No. 1 (January-February 1955) publication is to be semi-annual. The subscription price outside France is 1200 francs, airmail postage extra. Subscription can be taken by payment to the postal account (Compte Courant Postal de M. l'Agent Comptable de l'Office de la Recherche Scientifique et Technique Outre-Mer, No. 9061-95, Bureau de Paris, France) or by UNESCO coupons.